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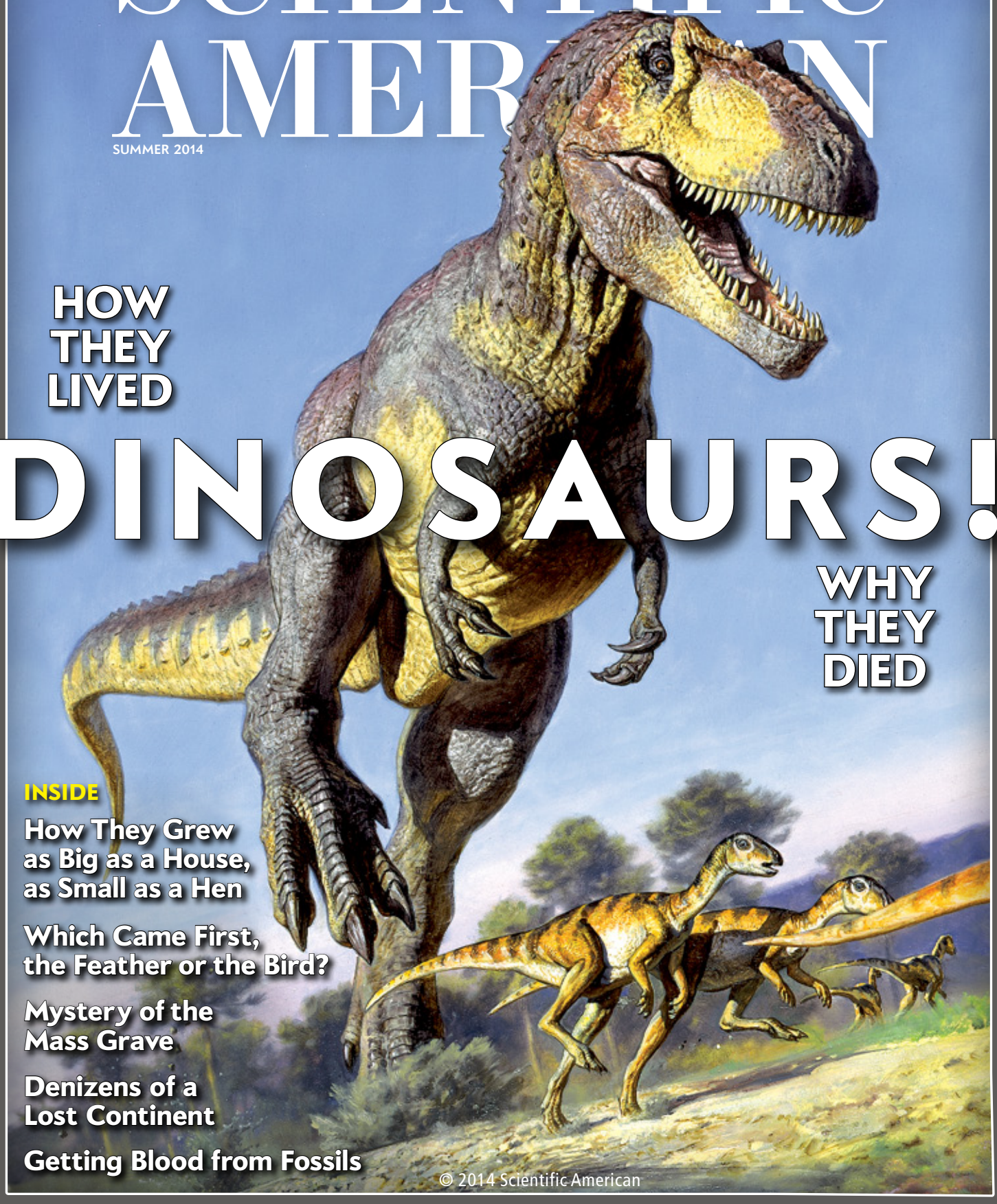

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Which Came First, the Feather or the Bird?

Mystery of the Mass Grave

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The Monsters We Adore

TERRIBLE LIZARDS. THAT'S WHAT THE WORD "DINOSAURS" MEANS. YET DINOSAURS ARE NOT true lizards, and they are not necessarily terrible either. What they are is endlessly fascinating—and still able to surprise us.

Paleontologists have overturned one misconception after another: As it turns out, dinosaurs were not necessarily sluggish and cold-blooded. Many dinosaurs had feathered skins long before the origin of birds. And not all dinosaurs were enormous: some were less than a foot long. Others, of course, grew to be more than 100 feet long, and growth lines in dinosaur bones are providing clues about how quickly these animals reached full size, as John R. Horner, Kevin Padian and Armand de Ricqlès explain in "How Dinosaurs Grew So Large and So Small," beginning on page 4. Even in the American West, where many of the earliest discoveries were made, there have been surprises. We now know, for example, that distinct communities of ancient behemoths once shared a relatively small landmass; Scott D. Sampson writes about their lives in "Dinosaurs of the Lost Continent," on page 20.

We still have much to learn about dinosaurs: the details of how they looked and sounded, exactly what they ate, and what kind of interactions they had with one another and with other species. For example, although recent research has revealed that *Tyrannosaurus rex* could bite down with tremendous force and then rake its teeth deeply through flesh and bone, paleontologists still are not sure whether *T. rex* was primarily a predator or a scavenger, as Gregory M. Erickson points out in "Breathing Life into *T. rex*." Turn to page 38.

Calling someone a dinosaur is supposed to be an insult, but it's a misguided one. These amazing creatures ruled the earth for tens of millions of years. Scientists now realize that even the long-necked, small-brained sauropods—once seen as awkward also-rans—thrived for nearly 150 million years; go to "Triumph of the Titans," by Kristina A. Curry Rogers and Michael D. D'Emic, starting on page 12, to learn about their secrets for success. Modern humans, by comparison, have been around for only a couple of hundred thousand years. And although most dinosaurs perished in a massive extinction about 66 million years ago, technically they are still around: Birds not only evolved from dinosaurs but also lived alongside them for a while, as Gareth Dyke writes in "Winged Victory," beginning on page 70. Some birds managed to survive the mass extinction.

Like the dinosaurs before us, humans are now the dominant species on the planet, but we, too, could face extinction—if not from an asteroid impact, then perhaps from precipitous climate change or nuclear warfare. Dinosaur fossils provide us with tantalizing hints of the fragility of existence—and of the capacity for adaptation.

Dawn Stover
Issue Editor
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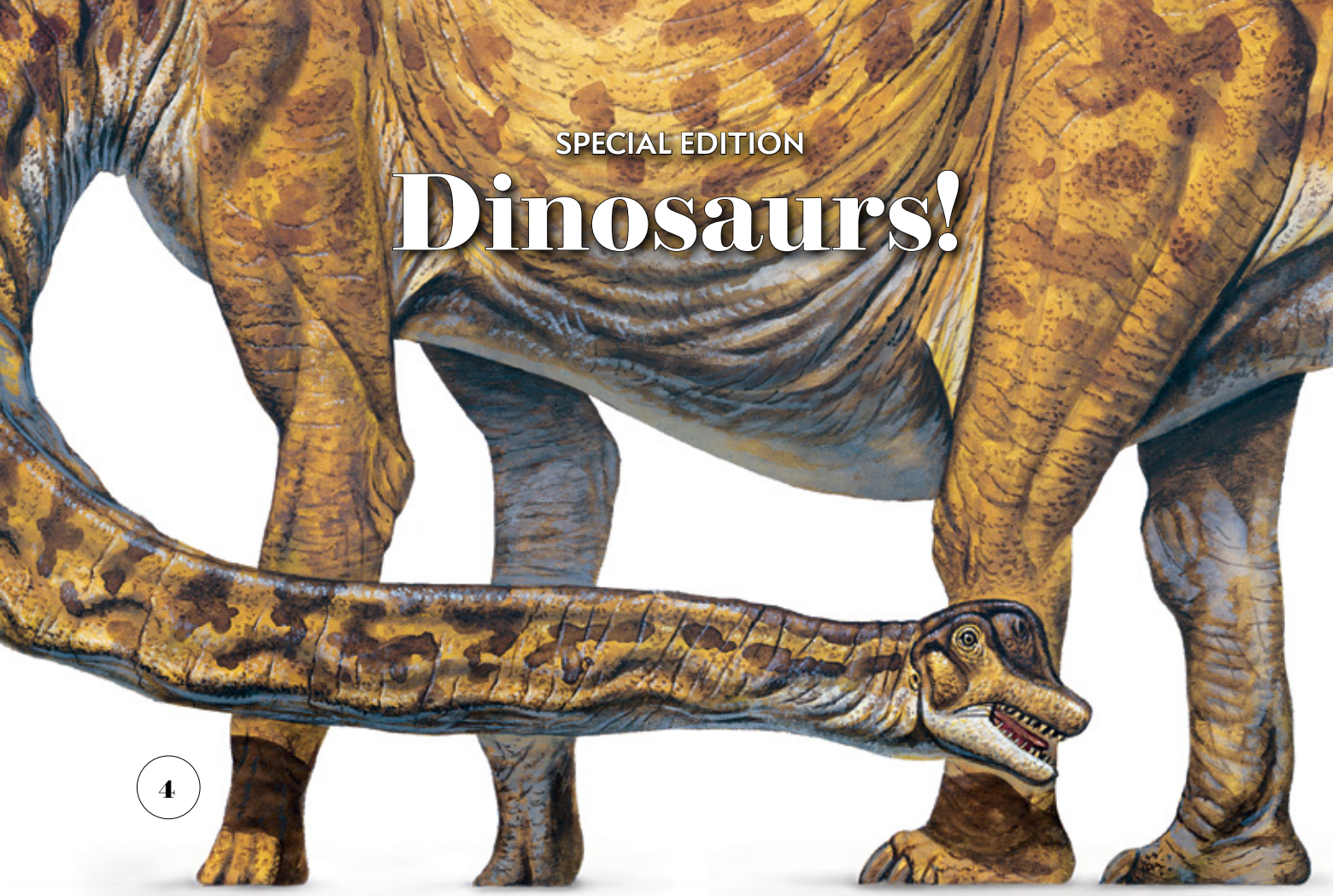
SPECIAL EDITION

Dinosaurs!



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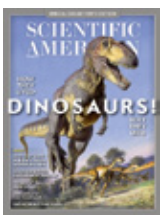

A carnivorous *Giganotosaurus* chases human-size plant eaters in Patagonia during the Cretaceous. Image by James Gurney.

MARK HALLETT (Brachiosaurus)

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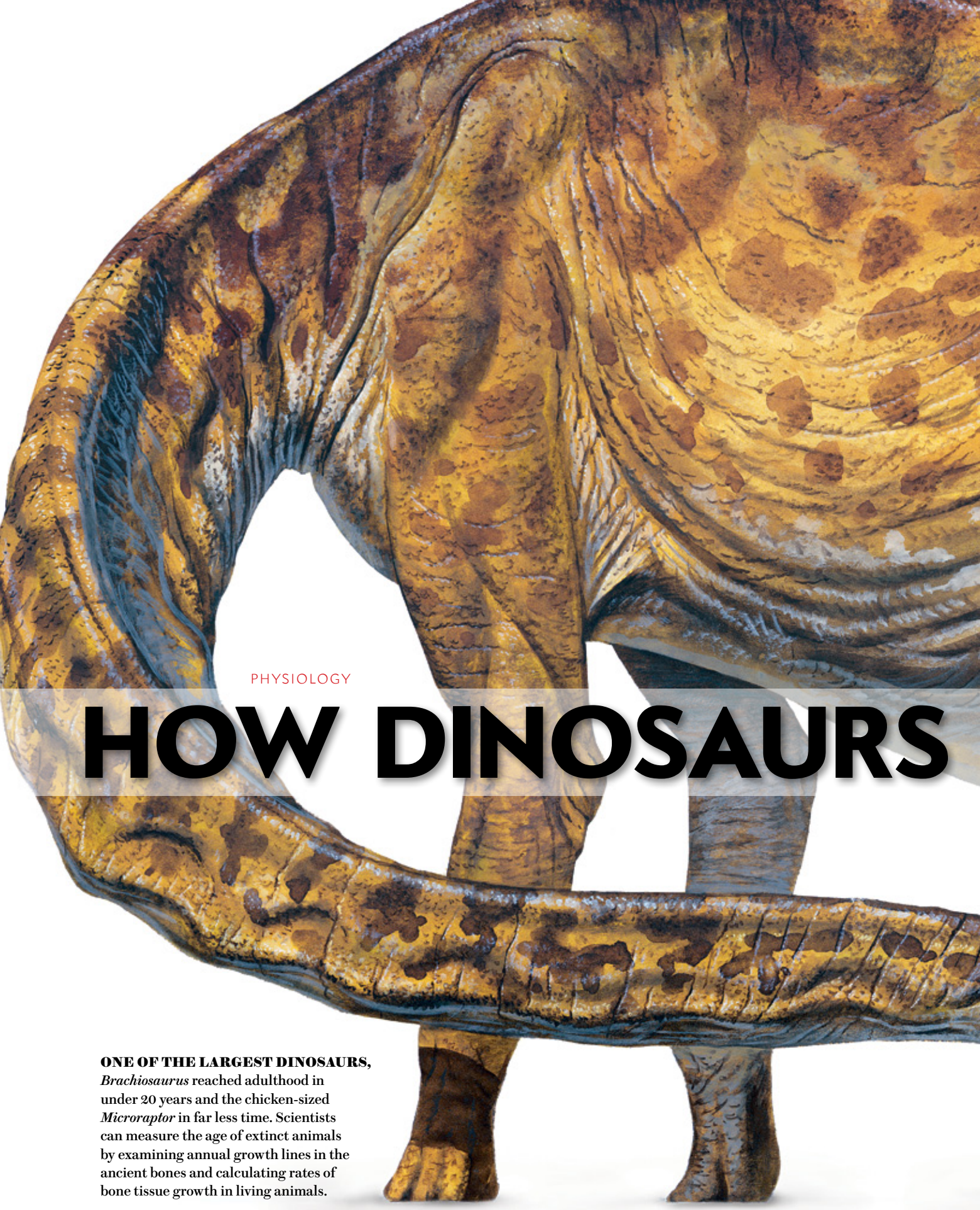

PHYSIOLOGY

HOW DINOSAURS

ONE OF THE LARGEST DINOSAURS, *Brachiosaurus* reached adulthood in under 20 years and the chicken-sized *Microraptor* in far less time. Scientists can measure the age of extinct animals by examining annual growth lines in the ancient bones and calculating rates of bone tissue growth in living animals.

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GREW SO LARGE AND SO SMALL

Lines and other structures in dinosaur bones reveal how these animals grew and how long they lived

By John R. Horner, Kevin Padian and Armand de Ricqlès

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MOST PEOPLE CAN STAND COMFORTABLY UNDER THE JAWLINE OF a mounted *Tyrannosaurus rex* or walk under the rib cage of a *Brachiosaurus* without bumping their head. *T. rex* is as big as the largest known African elephant, and *Brachiosaurus,* like other great sauropods, was much larger than any land animal alive today. We are so used to the enormous size of dinosaurs that we almost forget to think about how they grew to be so large. How long did it take them, and how long did they live? And does the way they grew tell us about the way their bodies worked?

Until relatively recently, we had no way to measure age in a dinosaur. Paleontologists had generally assumed that because dinosaurs were reptiles, they probably grew much as reptiles do today—that is, rather slowly. Thus, the thinking went, large dinosaurs must have reached very old ages indeed, but no one knew how old, because no living reptiles attain anything near the size of a dinosaur.

This attitude can be traced back to English paleontologist Sir Richard Owen. When he named the Dinosauria in 1842, he was putting a label on a very small, poorly known group of very large, unusual reptiles. Not only were they big, he said, but they were terrestrial, unlike the seagoing ichthyosaurs and plesiosaurs that had been known since the early 1800s. They had five vertebrae (backbones) connected to the hips, not two like living reptiles. And they held their limbs underneath their bodies, not sprawled out to the sides. Despite these differences, he continued, the anatomical features of their bones—the shapes, joints and muscle attachments—showed them to be reptiles. So they must have had a reptilian physiology—that is, a typically "cold-blooded," slow metabolism. The image stuck, and well into the 1960s dinosaurs were portrayed as sluggish, lumbering animals that must have grown slowly to great size in a sort of benign hothouse where huge beasts reigned and raged.

Yet evidence for the ages of dinosaurs, and so for how they must have grown, was there all the time—locked inside the bones themselves. Although paleontologists had known for many years that the bones of dinosaurs contain growth lines, something like the circumferential growth rings we see in trees, it was only in the second half of the 20th century that they began to use these growth lines and other structures inside the bones to figure out how these extinct animals actually grew.

THE BONES TELL THE STORY

LIKE THE RINGS IN TREES, the lines in the bones of dinosaurs were annual. But they aren't quite as simple to interpret. A tree carries nearly the entire record of its growth inside its trunk. Cut it down, and you can count the rings one by one from the center to the bark. Only the outer layer is making new wood; the inside is really deadwood. The center of a bone, in contrast, is a busy place. Cells called osteoclasts hollow out the center of a long bone, such as the femur (thigh) or tibia (shin), by breaking down existing bone and allowing its nutrients to be recycled. This center, or marrow cavity, is also the factory that produces red blood cells [*see box on opposite page*].

To accomplish these tasks, the whole bone constantly grows and changes throughout life. As a bone grows, new tissue is deposited on the outside, and in the long bones growth also occurs at the ends of the shafts. Meanwhile, in the marrow cavity, osteoclasts are eroding the bone that was deposited early in life, and other cells are making

IN BRIEF

Until recently, paleontologists had no way to measure the age of dinosaurs and thus to figure out how they grew, so they assumed that dinosaurs had a physiology similar to modern reptiles.

It turns out that this information has been locked in the animals' bones all along—many of the bones contain growth lines that are somewhat similar to the annual growth rings in trees.

Using these lines and other structures within the bones, scientists have now shown that dinosaurs grew to full size quickly—much in the way that birds and mammals do today and not at all like the more slowly growing living reptiles.

This fast growth implies that these ancient creatures had a high metabolic rate closer to that of warm-blooded animals than to cold-blooded reptiles.

PRECEDING PAGES: MARK HALLETT

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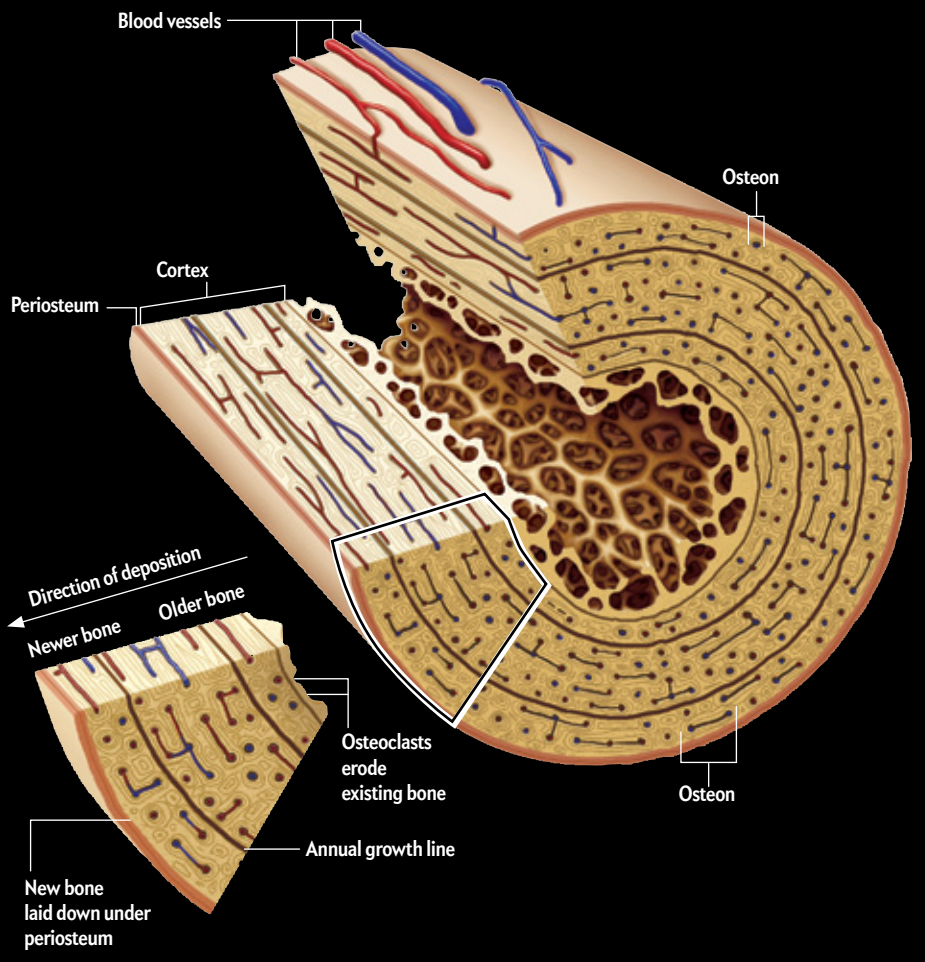
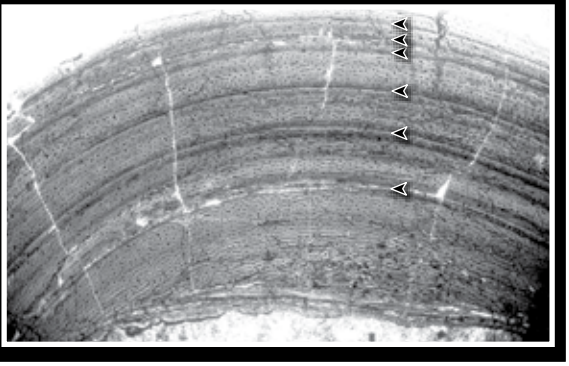
Reading a Dinosaur Bone

The bones of dinosaurs contain growth lines, somewhat similar to the annual rings in trees, although they are more complicated to interpret. The cortex of bone is built by minerals such as calcium phosphate and proteins such as collagen, which are carried by blood vessels. When the vascular canals, which contain the blood vessels, begin to deposit bone along their insides in concentric layers, they are called osteons. In the femur, or thighbone, and other long bones, growth is concentrated just underneath an outer membrane, the periosteum. Meanwhile the inner margin of the bone is being eaten away by osteoclast cells. A secondary series of osteons may invade preexisting bone, eroding it and depositing new bone. Because of all this activity, researchers cannot simply slice open a dinosaur bone and determine the age of the animal, but they can gain such information by performing various analyses of the rings and other features.



Growth Lines

The annual growth lines in the diagram above can be seen in the photograph of the inside of the femur of *Troodon*, a small carnivorous dinosaur. These lines (*arrows*) become more closely spaced toward the outside of the bone, which was deposited in the later period of the dinosaur's life—when the animal was growing at a slower rate, as we all do with advancing age.



SHAWN GOULD (*illustrations*); JOHN R. HORNER, KEVIN PADIAN AND ARMAND DE RICQLÈS (*photograph*)

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EVOLUTION

Early Birds

Do new insights about the rapid pace at which extinct dinosaurs grew give us any new information about the evolution of birds, the living dinosaurs? Why, for example, are birds so much smaller than extinct dinosaurs? Did they change their growth rates somehow? We began looking into these questions by examining the bone tissues of *Confuciusornis,* an ancient bird from the Early Cretaceous (125 million years ago) of China that appears on the avian family tree shortly after *Archaeopteryx,* the first known bird. The inner part of the bone tissues of the crow-sized *Confuciusornis* is of a fast-growing, fibro-lamellar type (like those of other dinosaurs), but toward the outside it becomes a slower-growing type—a sign that the growth rate waned after a short, youthful spurt. We compared these tissues with those of *Troodon,* a small raptorlike dinosaur about 1.5 meters long, which David J. Varricchio of Montana State University had studied. *Troodon* tissues indicate faster growth overall.

As *Confuciusornis* shows, to become small these ancient bird species truncated the juvenile burst of growth that was most rapid in other dinosaurs, which caused the birds in effect to become miniaturized. Miniaturization had an important influence on locomotion because the feathers that were present on the forelimbs of the closest dinosaurian relatives of birds would have been more likely to help these smaller animals become airborne. Small animals can flap their wings faster than large ones, and in a smaller animal the wing loading (the ratio of weight to wing area, or how much a given unit of area has to carry) will be proportionally smaller and so aerodynamically more advantageous.

But birds today reach full size quickly, usually in weeks to months. What changed? It appears that after slowing early in their evolution, birds over time sped up their growth rate again—to rates that are often even faster than those in extinct dinosaurs. Some years ago Anusuya Chinsamy-Turan, now at the University of Cape Town in South Africa, and her colleagues studied the bone tissue of early birds a bit farther along the evolutionary tree than *Archaeopteryx* and *Confuciusornis.* These Late Cretaceous birds included a primitive enantiornithine, the flightless *Patagopteryx,* the diving *Hesperornis* and the ternlike *Ichthyornis* [*see box on pages 10 and 11*]. They, too, grew more slowly than dinosaurs, but the forms closer to living birds had tissues that indicated somewhat more rapid growth than in the very early birds.

Close to the Cretaceous-Paleogene boundary, about 66 million years ago, growth rates increased substantially, so much so that all living birds—even the ostrich—attain full size within less than a year (seven days in the case of the sparrow). Only examination of birds from the Early Paleogene will tell us whether the living groups of birds acquired their habit of rapid growth to adult size gradually or relatively suddenly. *—J.R.H., K.P. and A.d.R.*

D I N O S A U R S !

secondary bone tissue along the perimeter of the cavity or invading the cortex (outer layer) of the remaining bone to remodel it.

This activity at the center of the bone often erodes the record of growth during the youngest stages of an individual's life. Consequently, it is difficult to cut open the bone of a dinosaur and find a complete record of growth just by counting the rings. So we reconstruct the early history of the bone in several ways. One is to use the bones of younger individuals to fill in the record. These younger bones contain the tissues that have been eroded in older bones. By examining these tissues and counting the growth lines, we can approximate the number of years that are missing from the older bones. When we have no juveniles available, we can "retrocalculate" the number of growth lines by examining distances between preserved growth lines.

In 2004 we tried retrocalculation on the most famous dinosaur of all: *T. rex.* The Museum of the Rockies at Montana State University has a dozen specimens of this giant carnivore, and seven of them have reasonably well preserved hind-limb bones that allowed us to make thin slices that can be examined under a microscope.

The microscopic slides of *T. rex* bones revealed only four to eight preserved growth lines. Others, near the center, had been obscured by the growth of secondary bone tissue. Even more striking, the marrow cavity is so large in these dinosaurs that two thirds of the original bone cortex is eroded away. We also noticed that in some individuals the space between the growth lines suddenly became very small toward the outermost surface of the bone. We had seen this before in other dinosaurs, such as the plant-eating duckbill *Maiasaura*. It signifies the end of active growth, when the animal reached full size.

Our retrocalculations estimated that *T. rex* took 15 to 18 years to attain full size, which is to say a hip height of three meters (10 feet), a length of 11 meters (34 feet), and a weight of 5,000 to 8,000 kilograms (five to eight tons). (We were pleased to see that our estimates matched those of Gregory M. Erickson of Florida State University and his colleagues, which were completed at about the same time.) If that seems like rapid growth, it is. At least, for a reptile. It turns out that dinosaurs grew much faster than other living or extinct reptiles do.

For example, Erickson and Christopher A. Brochu of the University of Iowa charted the growth of the giant crocodile *Deinosuchus,* which lived during the Cretaceous period, some 75 million to 80 million years ago [*see bottom illustration on page 10*]. These huge reptiles reached estimated lengths of 10 to 11 meters. Examining the growth lines in the skin armor of the neck, Erickson and Brochu determined that such an animal required nearly 50 years to achieve this length—three times as long as it took *T. rex* to get to the same size. A closer comparison for *T. rex* proves to be the African elephant, which reaches about the same mass (5,000 to 6,500 kilograms) in 25 to 35 years. So *T. rex* grew to its adult size even faster than an elephant does.

Further research showed that *T. rex* is not unusual for dinosaurs—except that it actually grew a little bit more slowly for its size than other large dinosaurs did. Anusuya Chinsamy-Turan, now at the University of Cape Town in South Africa, found that the plant-eating *Massospondylus* took about 15 years to reach a length of two to three meters. Erickson and Tatyana A. Tumanova of the Paleontological Institute in Moscow found that the small ceratopsian (horned) *Psittacosaurus* was mature at 13 to 15 years. And we calculated that

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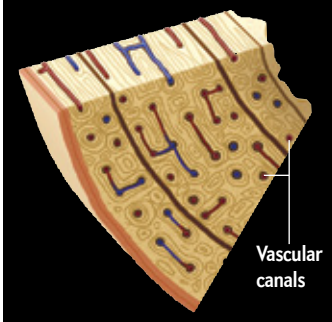
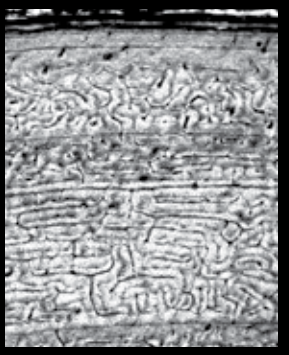
COMPARISON

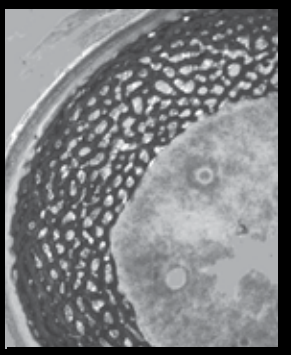
Dinosaurs Didn't Grow Like Reptiles



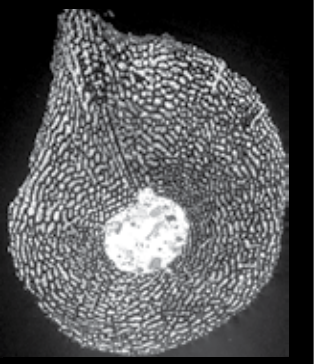
Fibro-lamellar bone tissue



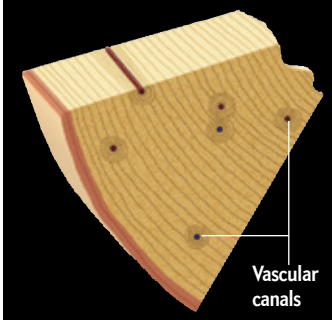
Elk



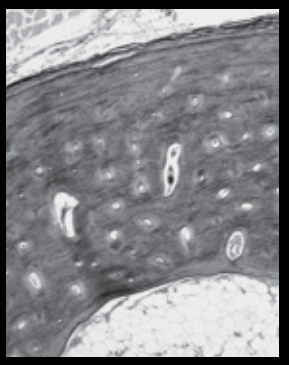
Ostrich



Maiasaura



Lamellar-zonal bone tissue



Alligator

Dinosaur bones, on the inside, look much like the bones of large birds and mammals (*above*). These animals, unlike reptiles (*left*), lay down a type of bone tissue called fibro-lamellar, which grows on a scaffold of minerals and collagen fibers that are produced in discrete layers. Their bone tissue is usually very well vascularized. Lots of blood vessels imply rapid deposition of tissue and so fast growth. The elk and alligator bones shown here are of nearly mature individuals. Toward the outside of the bone are far fewer vascular canals, reflecting a slowing of growth. The duckbill *Maiasaura* and the ostrich bones are from near-hatchling individuals. The vascular spaces in their bones are copious, indicating very rapid growth that has not yet settled into the fibro-lamellar pattern.

Maiasaura reached adulthood at between seven and eight years, by which time it was seven meters long. The giant sauropods ("brontosaur" types) outdo all the others, though: Martin Sander of the University of Bonn in Germany discovered that *Janenschia* reached maturity at about 11 years, although it continued to grow substantially after that. Frédérique Rimblot-Baly and her colleagues, then at the University of Paris VII, determined that *Lapparentosaurus* attained full size before it was 20 years old. Kristina A. Curry Rogers, now at Macalester College, found that *Apatosaurus* (more familiarly known as *Brontosaurus*) matured in eight to 10 years—an annual weight gain of nearly 5,500 kilograms.

INSIDE A DINOSAUR BONE

WHY SHOULD DINOSAURS grow more like elephants than like giant crocodiles? And what does this mean for other aspects of their biology? To answer these questions, we have to look inside a dinosaur bone at the kind of tissues it laid down.

The tissue in a typical long bone of a dinosaur is primarily a type called fibro-lamellar: it is highly fibrous or "woven" in texture, and it forms around a matrix of poorly organized collagenous fibers that is well supplied with blood vessels. In contrast to what we would expect in conventional reptiles, this is the same kind of tissue that predominates in the bones of large birds and large mammals, which grow to full size faster than typical reptiles do. A crocodile bone, on the other hand, is formed mostly of lamellar-zonal tissue—compact, highly mineralized bone that contains more regularly organized fibers and much sparser, smaller vascular canals. Furthermore, the growth lines in crocodile bones are more tightly spaced than those in dinosaur bones, another indication that crocodile bones grow more slowly [*see box above*].

The late Rodolfo Amprino, then at the University of Turin in Italy, recognized in the 1940s that the type of tissue laid down in a bone at any given place or time during growth was mainly a function of how fast the tissue was growing at that point. Fibro-lamellar tissue, no matter where or when it is deposited, reflects locally rapid growth, whereas lamellar-zonal tissue signals slower growth. An animal can lay down either of these tissues at different times—as the growth strategy warrants. The type of tissue that predominates through the animal's life provides the best guide to its growth rate.

One difference between dinosaurs, on the one hand, and crocodiles and other reptiles, on the other, is that dinosaurs deposit fibro-lamellar tissue all through growth to adult size, whereas other reptiles switch very soon to lamellar-zonal bone. We inferred from this that dinosaurs sustained more rapid growth until the adult stage because there would be no other good explanation for the persistence and predominance of fibro-lamellar tissue.

The pace at which dinosaurs grew was assessed in a different way by Erickson, Rogers and Scott A. Yerby, then at Stanford University.

SHAWN GOULD (*illustrations*); JOHN R. HORNER, KEVIN PADIAN AND ARMAND DE RICQLÈS (*photographs*)

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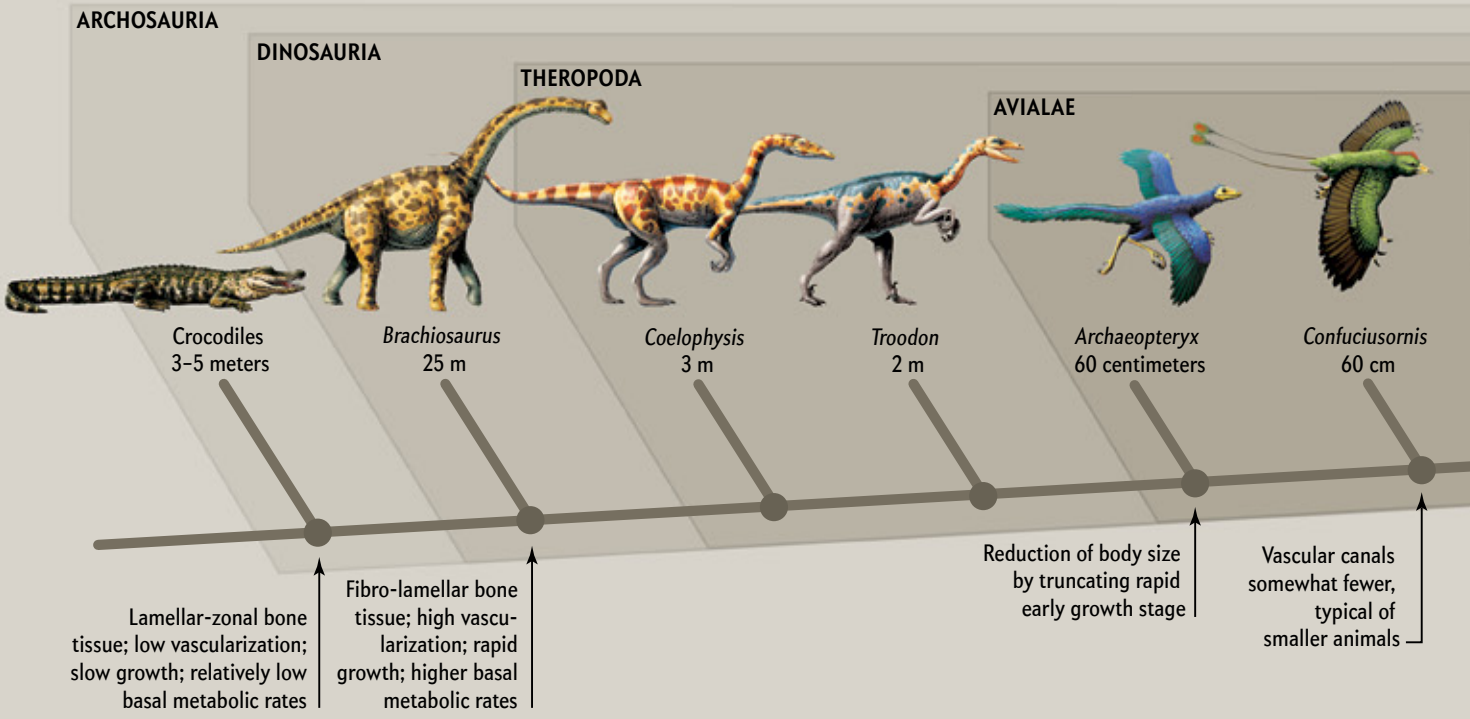
CHART

Bone Growth and Evolution in Birds

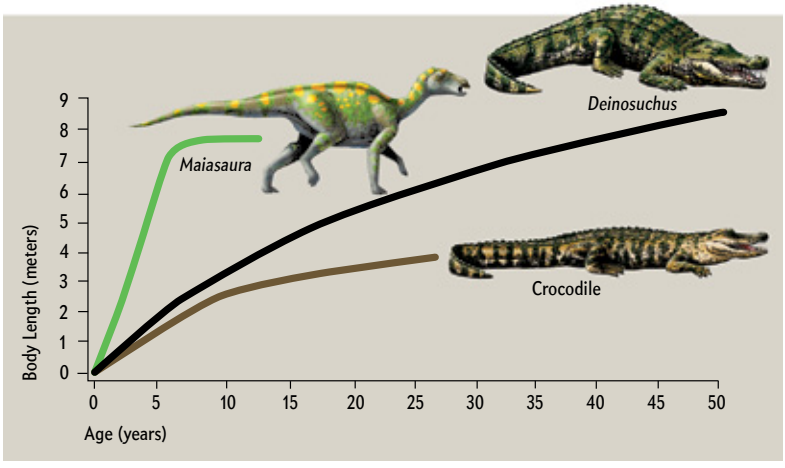


Using estimates of body mass of dinosaurs, they plotted the animals' mass against time to derive growth curves for a variety of species and compared the curves with those for other groups of vertebrates. They found that all dinosaurs grew faster than all living reptiles, that many dinosaurs grew at rates comparable to those of living marsupials, and that the largest dinosaurs grew at rates comparable to those of rapidly maturing birds and large mammals. We confirmed their results for body mass with our own studies using length.

In one sense, such findings were not unexpected. Many years ago Ted J. Case, then at the University of California, Los Angeles, showed that within any group of vertebrates, larger species reach adult size in a longer time but grow more quickly to do so. What was surprising is that dinosaurs grew as fast as they did.

We were curious about when in the course of their evolution dinosaurs acquired this habit of rapid growth, so we plotted our estimated growth rates on a cladogram, or diagram of relationships, that was built on hundreds of independent characteristics from all parts of the skeleton. We added the estimated growth rates for pterosaurs (flying reptiles closely related to dinosaurs, which grew much like them), crocodiles and their extinct relatives, and lizards. We put birds among the dinosaurs because birds evolved from dinosaurs and so are technically included with them.

For added help in estimating the growth rates of dinosaurs, we looked at living birds, which show the same range of tissues expressed in dinosaur bones. Jacques Castanet and his colleagues, then at Pierre and Marie Curie University in Paris, injected mallard ducks with solutions that would stain the growing bones. By using different colors at different times, they



GROWTH CURVES show that even the largest dinosaurs were actually teenagers when they reached their huge sizes. They grew to adult size far faster than conventional reptiles do.

SHAWN GOULD (*illustrations*); JEN CHRISTIANSEN (*top cladogram and bottom graph*)

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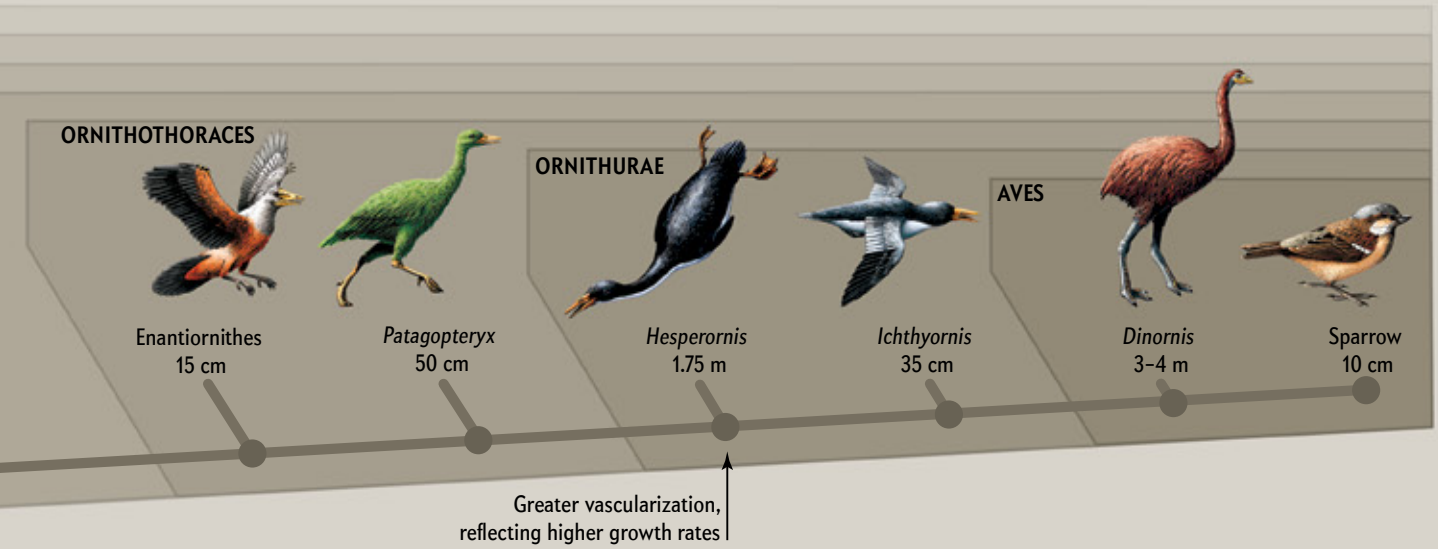

Dinosaurs, from their beginning, had bone tissues that differed greatly from those of other reptiles. Their bones grew more rapidly, as in birds and mammals of today. When the first birds (Avialae) evolved, their substantial reduction in size was a result of slower growth of their bone. But their growth was still more rapid than in other reptiles. Then, as the living bird groups (Aves) began to emerge, growth accelerated again, so that pigeon-sized birds matured in weeks instead of months. All birds today, even the ostrich, reach adult size within a year, and most do so much more quickly—the sparrow in seven days. When birds evolved, they slowed down their growth rates at exactly the time when growth is highest in their dinosaur ancestors, their juvenile period, effectively miniaturizing them as adults.

were able to measure rates of weekly growth in the sacrificed birds. Using these calibrations, we determined that dinosaurs and pterosaurs grew at much higher rates than other reptiles.

UNCONVENTIONAL REPTILES

THE STUDY OF DINOSAUR BONES has told us a great deal about the evolution of some of the major features of these animals. About 230 million years ago, in the early part of the Triassic period, the lineage that would produce dinosaurs, pterosaurs and their relatives split from the lineage that would produce crocodiles and their relatives. The dinosaurian lineage soon acquired sustained elevated growth rates that set them apart from other reptiles. This speedy growth may have played a role in the success that dinosaurs and pterosaurs enjoyed toward the end of the Triassic, when so many species with more typical reptilian bone structure became extinct.

The high growth rates of dinosaurs also give us a firmer idea about their metabolic features. The higher the metabolic rate—that is, the more energy devoted to building up and breaking down bone and other tissues—the faster the tissues will grow. So evidence of sustained rapid growth, even into late juvenile and subadult stages, implies that the animals in question had relatively high basal metabolic rates, probably more like those of birds and mammals than like those of today's reptiles. This suggests that they were much more likely to have been warm-blooded, in a general sense, than cold-blooded, but it is difficult to know the details, such as body temperature and how much it varied. Clearly, many questions remain. Dinosaurs were perhaps even more unusual creatures than we had previously thought—not exactly like any animals of today and certainly not conventional reptiles. If anyone ever discovers a five-ton living bird, a lot of these questions will be settled. SA

John R. Horner, Kevin Padian and **Armand de Ricqlès** have worked together on investigations of dinosaur bones for more than 20 years. Horner is curator of paleontology at the Museum of the Rockies and Regents Professor of Paleontology at Montana State University. Padian is professor of integrative biology and curator of the Museum of Paleontology at the University of California, Berkeley. De Ricqlès is emeritus professor at the Collège de France in Paris, where he occupied the chair in historical and evolutionary biology (1996–2010); his CNRS team at the University of Paris VII studies bone formation and skeletal tissues.

MORE TO EXPLORE

Dinosaurian Growth Rates and Bird Origins. K. Padian, A. J. de Ricqlès and J. R. Horner in *Nature,* Vol. 412, pages 405–408; July 26, 2001.

Dinosaurian Growth Patterns and Rapid Avian Growth Rates. G. M. Erickson, K. Curry Rogers and S. A. Yerby. Ibid., pages 429–433.

Age and Growth Dynamics of *Tyrannosaurus rex*. J. R. Horner and K. Padian in *Proceedings of the Royal Society B,* Vol. 271, No. 1551, pages 1875–1880; September 22, 2004.

Growth in Small Dinosaurs and Pterosaurs: The Evolution of Archosaurian Growth Strategies. K. Padian, J. R. Horner and A. de Ricqlès in *Journal of Vertebrate Paleontology,* Vol. 24, No. 3, pages 555–571; September 2004.

What's Inside a Dinosaur Bone? K. Padian in UCMP News (University of California, Berkeley); September 2004. Online at www.ucmp.berkeley.edu/museum/ucmp_news/2001/5-01/dinosaur1.html

Physiology. K. Padian and J. R. Horner in *The Dinosauria.* Second edition. Edited by D. Weishampel, P. Dodson and H. Osmólska. University of California Press, 2004.

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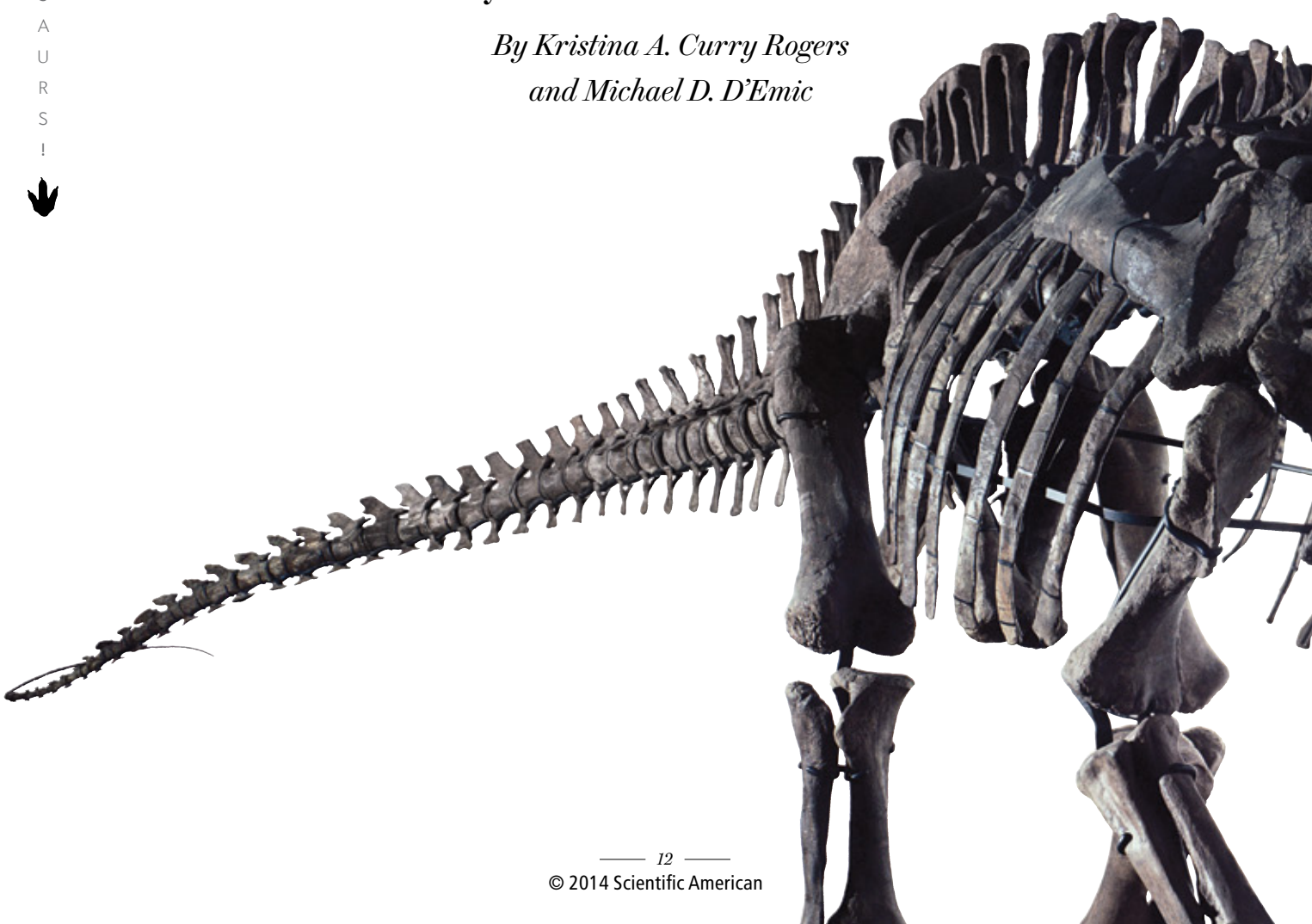
EVOLUTION

TRIUMPH OF THE TITANS

The long-necked dinosaurs known as sauropods, once seen as icons of extinction, thrived for millions of years all around the world

By Kristina A. Curry Rogers and Michael D. D'Emic



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APATOSAURUS, **the proper scientific name for the famous *Brontosaurus*, exhibits the classic sauropod silhouette: a long spinal column, tapered on both ends, topped with a small-brained skull and balanced on four pillarlike legs. Over the course of their long reign, sauropods evolved various body sizes and different teeth and snout shapes, but their basic architecture stayed the same.**

Photograph by Christopher Griffith

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EVER SINCE FOSSILS OF THE BEHEMOTH, LONG-NECKED DINOSAURS KNOWN as sauropods surfaced in England more than 170 years ago, they have awed and confused scientists. Even when the great English anatomist Sir Richard Owen recognized in 1842 that dinosaurs constituted a group of their own, apart from reptiles, he excluded the gigantic bones later classified as sauropods. Instead he interpreted them as belonging to a type of aquatic crocodile, which he had named *Cetiosaurus,* or "whale lizard," for the enormous size of its bones. Nearly 30 years later, in 1871, University of Oxford geologist John Phillips would report the discovery of a *Cetiosaurus* skeleton sufficiently complete to reveal that, far from being an aquatic crocodile, the animal spent at least some of its time on land.

Phillips's assessment caused considerable consternation among paleontologists for decades—they just could not conceive how such a massive animal could support its weight on land. Because sauropods were perceived as animals without a place, unsuited for land or sea, they came to be seen as unwieldy, overgrown, archaic herbivores fated for rapid extinction or, at least, marginalization by more "advanced" dinosaurs. As recently as 1991, scientists argued that sauropods were far from the apex of dinosaur success and only flourished in the absence of more specialized plant-eating dinosaurs. In this view, these giants of the Jurassic period, between about 200 million and 145 million years ago, gave way to bigger-brained, better-adapted herbivores in the Cretaceous, between some 145 million and 66 million years ago, such as the duck-billed hadrosaurs and horned ceratopsians, which outcompeted the sauropods and pushed them to the fringe.

Relegated to the Southern Hemisphere, so the story goes, only a handful of sauropod stragglers held out to the end of the Cretaceous, when an asteroid impact brought the dinosaur era to a close.

This view of maladapted sauropods plodding along to obscurity was itself destined for extinction. Recent discoveries of sauropods from locales around the world—more than 70 new species since 2002—have revealed an extraordinarily resilient group that flourished for millions of years at the observed limits of terrestrial body size. Thanks to such finds and new analytical tools for evaluating them, scientists have begun to answer key questions about how sauropods reproduced, how they grew, what they ate and how they adapted to dramatic environmental change. These revelations have changed almost everything that we thought we knew about this iconic group.

BEYOND THE CLASSICS

LIKE MOST PEOPLE, the two of us first encountered the long-necked giants of the dinosaur world amid the cacophony of kid-filled natural history museums. Towering above the din of excited field-trippers stood the stately sauropod: longer than two school buses, its neck and skull stretched far above the crowds and the other dinosaurs. Even in dust-covered silence, the bones inspired awe. Most of the classic sauropods—such as *Diplodocus, Camarasaurus* and *Apatosaurus*—made their debut in the late 1800s, and by the turn of the century every major natural history museum had to have one. Jurassic sauropod bones flowed into museums in such great numbers that it is still possible to find shelves of these fossils in the bowels of their collections, encased in plaster field jackets, waiting to be opened and studied.

But those classic sauropods represented only a small fraction of the diversity of this group. The story of how sauropods originated and how they evolved into so many forms over their 150-million-year evolutionary history begins even before their appearance—about 210 mil-

IN BRIEF

Paleontologists traditionally viewed the long-necked, small-brained giant dinosaurs referred to as sauropods as doomed creatures unfit for life on land or in the water.

Recent discoveries have upended that scenario, revealing that sauropods prospered for nearly 150 million years.

The secrets of their success seem to have been their mix of mammal-like and reptilelike traits, combined with an ability to adapt to a changing world.

PRECEDING PAGES: PHOTOGRAPHED ON LOCATION AT CARNEGIE MUSEUM OF NATURAL HISTORY

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lion years ago in the Late Triassic, a time when the world witnessed an extinction event of other reptile groups that cleared the path for dinosaurs and their subsequent dominance of terrestrial ecosystems.

The oldest known dinosaurs in the fossil record are small-bodied, bipedal animals whose remains were found in roughly 230-million-year-old sediments in the Southern Hemisphere; these animals would eventually evolve into the more familiar sauropods and theropods (such as *Tyrannosaurus rex*). Paleontologists have found characteristic trackways of true sauropods—with their quadrupedal posture and elephantine feet—dating to around 225 million years ago in North America and in Argentina. The oldest hints of their massive skeletons are just a little younger, represented by creatures such as *Isanosaurus* from Thailand, *Gongxianosaurus* from China and *Vulcanodon* from Zimbabwe. These early species already bear the signature sauropod stamps: they were walking backbones (many sauropod species have more than 100 vertebrae), with long, tapering necks and tails, tiny skulls, and pillarlike limbs made for bearing serious weight. That basic architectural plan would persist in sauropods for their entire evolutionary duration, making them among the most recognizable of any dinosaur group.

Sauropods did not stagnate, however. Their body plan got more elaborate as time played on, with plate tectonics helping to drive the global diversification of their lineages. Sauropod diversity waxed and waned throughout the evolutionary history of the group—right up to the end of the dinosaur era. These recurrent spikes in diversity contradict the long-standing view that sauropods hit their short-lived prime in the Jurassic and limped along to their nadir in the Cretaceous. Instead we see important sauropod groups, such as the stocky titanosaurs and the shovel-faced rebbachisaurids, flourishing long after this presumed Jurassic heyday. Even in the twilight of dinosaur times during the Late Cretaceous, sauropods were diverse and still living large.

EVEN IN THE TWILIGHT OF DINOSAUR TIMES, SAUROPODS WERE DIVERSE AND STILL LIVING LARGE.

SIZING UP SAUROPODS

NEW DISCOVERIES HAVE SHOWN that sauropods were successful in terms of geographical range, diversity and the longevity of lineages. But what exactly were their strategies for getting by in the world? The answer seems to be that they made use of a special mix of reptilelike and mammal-like characteristics, which merged to create unique organisms. Although Owen was wrong in thinking that sauropods were lizards, in this respect his "whale lizard" name turned out to be fairly apt after all.

In their reproductive habits, sauropods, like all dinosaurs and most reptiles, hatched from eggs. The first concrete evidence for sauropod reproductive biology came from roughly 80-million-year-old deposits at Auca Mahuevo in Argentina, where in 1997 Luis Chiappe of the Natural History Museum of Los Angeles County and his colleagues found a sauropod nesting ground containing thousands of eggs. Inside some of the eggs, the researchers found the first known embryos of sauropods, some of which preserve fossilized skin and egg membranes.

These nesting traces provide clear evidence that titanosaur sauropods laid 20 to 40 spherical eggs per clutch in excavated depressions. The eggs are relatively small, averaging 13 to 15 centimeters in diameter, about the size of a grapefruit. The abundance of nests in the same layers at Auca Mahuevo suggests that the titanosaurs there associated in large groups and nested at the same area at least six times. Still, no convincing evidence exists that they sat on the eggs or cared for the young once they hatched. In fact, the proximity of the nesting structures to one another suggests that these titanosaurs were hands-off parents. Unlike other large-bodied vertebrates, such as elephants and whales, in which parents invest heavily in raising a single offspring, sauropods apparently stuck with the typical reptilian pattern of producing many offspring that were then left to fend for themselves.

Although sauropod parental investment hewed to the reptilian norm, the growth rates of these animals did not. Sauropods had the furthest to grow from newborn to adult of any animal ever to live. Baby sauropods were less than half a meter long and weighed less than 10 kilograms. As adults, the largest sauropods attained body lengths of 30 meters and body masses between 25,000 and 40,000 kilograms or more. For comparison, the average baby African elephant weighs around 120 kilograms at birth and reaches an adult weight of 2,268 to 6,350 kilograms. Most early dinosaur researchers simply extrapolated reptilian growth rates to estimate sauropod growth history. In this model, even smaller sauropods would have taken until age 60 to experience their first growth plateau and more than a century to reach adult size. That would mean waiting until age 60 to reproduce—risky business for any animal that stays relatively small and predator-prone for a big part of life.

A different perspective on sauropod development began to emerge in the 1960s, when Armand de Ricqlès, now emeritus at the Collège de France in Paris, began to study the internal microstructure, or histology, of bone for insights into the life history of dinosaurs and other extinct animals. The patterns of bone mineral, the density and architecture of the cavities left behind by blood vessels, and the degree of bone remodeling are all preserved in fossil bones. These features indicate that sauropod growth rates soared through most of life and that they were generally faster than the growth rates of reptiles and on par with those of living large-bodied mammals, many of which mature within decades. Therefore, sauropods did not have to live for centuries to become giants.

With such rapid growth rates and enormous adult body sizes, sauropods must have had prodigious appetites. Indeed, one of the most perplexing mysteries of sauropod biology is how these giants gathered enough plant matter to survive, much less thrive, for so long. Studies of sauropod feeding have focused on tooth shape, microscopic wear marks, jaw muscle reconstructions, and analyses of the biomechanics involved in opening and closing the jaw. This research has revealed that different sauropods employed distinctive feeding methods—some bit off tough vegetation, whereas others cropped or clipped softer plants.

Researchers generally agree that sauropods did not do a lot of chewing and thus most likely required some "postmouth" processing to break down plant food into usable energy. The most commonly cited solution to this need for extra processing is the use of gastroliths—or stomach stones, as they are popularly known. Polished stones often turn up in sauropod-bearing rock formations in western North America, and scientists have long hypothesized that these stones are analogous to the gastroliths that some modern vertebrates, such as certain birds, ingest to help grind up food and aid in digestion. In 2007, however, Oliver Wings, now at the Niedersächsischen Landesmuseums Hannover in Germany, and Martin Sander of the University of

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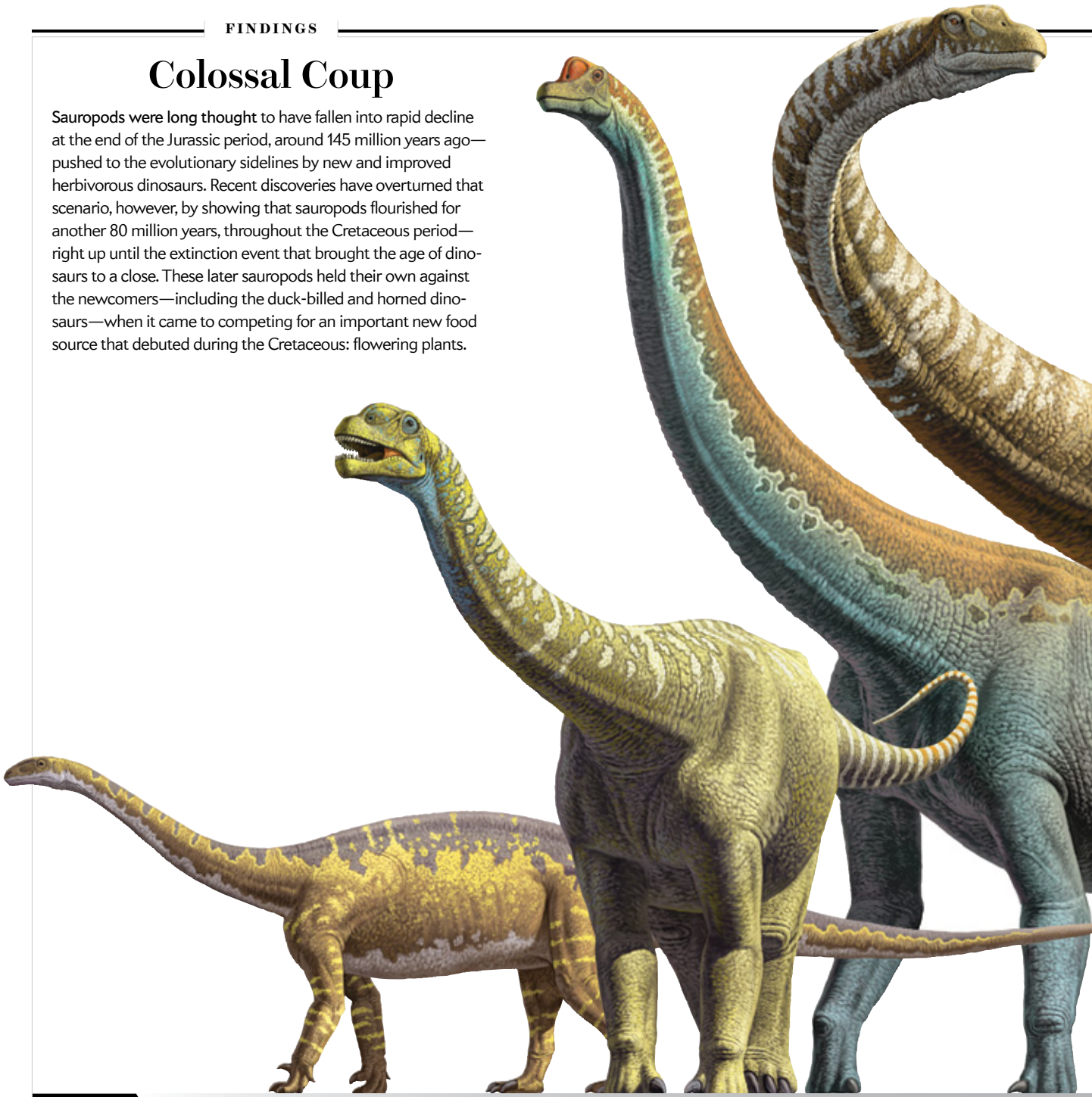
Colossal Coup

Sauropods were long thought to have fallen into rapid decline at the end of the Jurassic period, around 145 million years ago—pushed to the evolutionary sidelines by new and improved herbivorous dinosaurs. Recent discoveries have overturned that scenario, however, by showing that sauropods flourished for another 80 million years, throughout the Cretaceous period—right up until the extinction event that brought the age of dinosaurs to a close. These later sauropods held their own against the newcomers—including the duck-billed and horned dinosaurs—when it came to competing for an important new food source that debuted during the Cretaceous: flowering plants.



Illustrations by Raúl Martin, Graphics by Jen Christiansen

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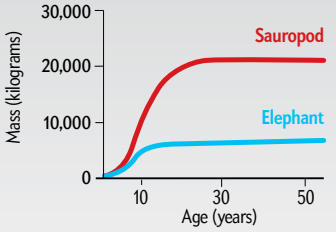
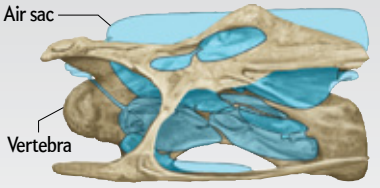
Survival Tricks

Sauropods benefited from a host of adaptations to living large on land, thus allowing them to reach sizes unequaled by any terrestrial animal since.

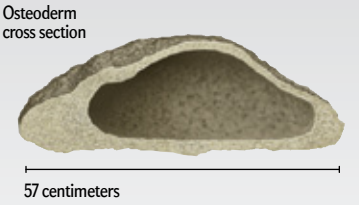
Unlike most reptiles, sauropods grew fast—akin to modern terrestrial giants, such as elephants—and would have reached adult size in a few decades.

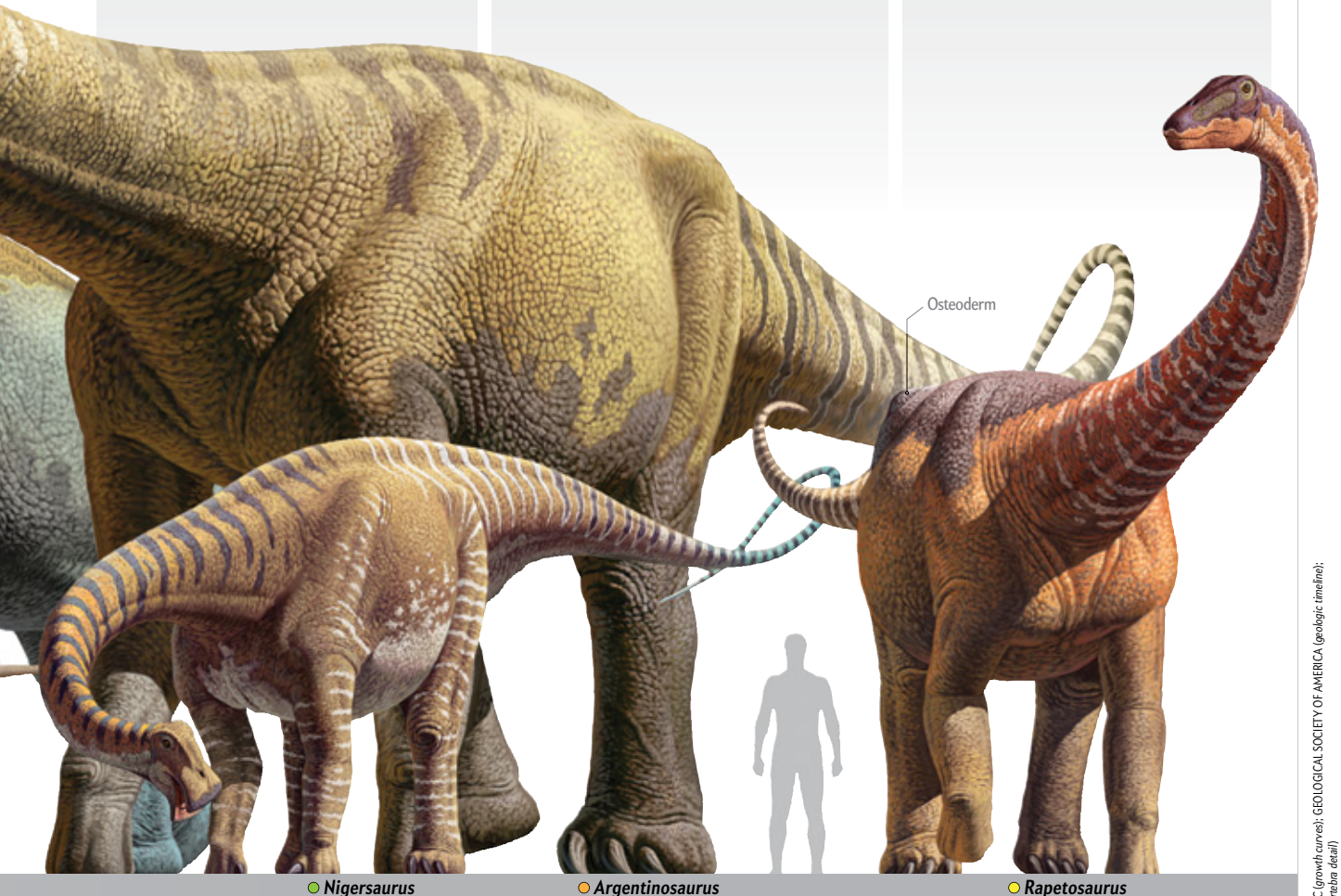


Hollow vertebrae would have lightened sauropod bodies and may have permitted the expansion of air sacs from the lungs that could have allowed them to take in more oxygen with each breath.

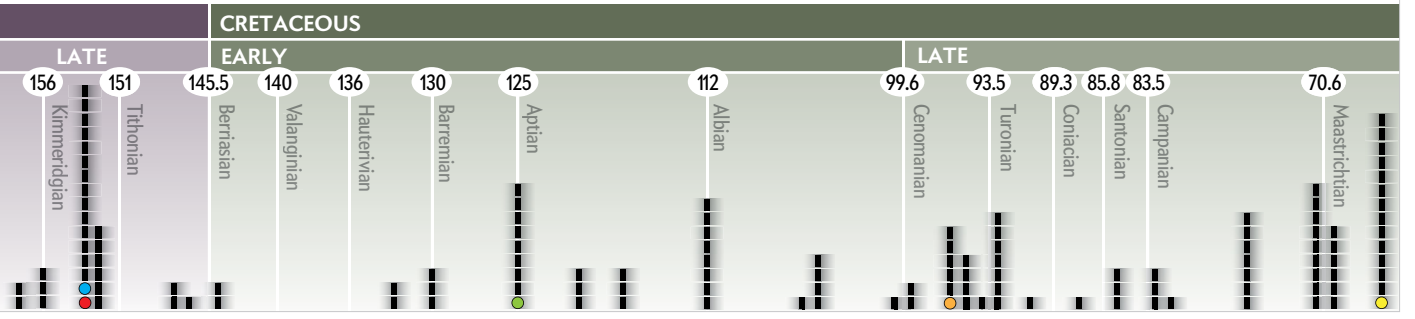


Bony plates called osteoderms, which were embedded in the skin of some sauropods, may have served as mineral reserves in hard times. As an animal aged, its osteoderms grew hollow from donating their calcium to the blood.





Nigersaurus Argentinosaurus Rapetosaurus



SOURCES: KRISTINA A. CURRY ROGERS AND MICHAEL D. D'EMIC (*growth curve*); GEOLOGICAL SOCIETY OF AMERICA (*geologic timeline*); DANIELA SCHWARZ-WINGS *Museum of Natural History, Berlin* (*vertebra detail*)

D I N O S A U R S !

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SNACK-SIZE SAUROPODS: Sauropods may have been untouchable as adults, but as babies they were highly susceptible to predators large and small. In 2010 Jeffrey Wilson of the University of Michigan and his colleagues described a clutch of sauropod eggs from India that includes a fossilized 3.5-meter-long snake coiled around and crushing one of them, alongside a tiny sauropod hatchling—as shown in the artist's reconstruction above. Several such examples from their field area of snakes associated with dinosaur eggs support the idea that these snakes frequented sauropod nesting grounds and feasted on eggs and hatchlings.

Bonn in Germany took the notion of sauropod gastroliths to task in an experimental analysis of how gizzard stones in living birds are processed and degraded. Their study showed that purported sauropod gastroliths lack the surface texture expected when compared with the true gastroliths of birds. Moreover, evidence of gastroliths discovered inside sauropod body cavities was scarce and equivocal. They thus concluded that, like modern big herbivorous animals such as rhinos, sauropods relied on microbial fermentation in their incredibly elongated digestive systems, not gastroliths, to extract energy from plants.

Additional insights into sauropod feeding strategies have come from studies of their most distinctive trait: that trademark long neck. Conventional wisdom held that the animals used their necks to dine in the treetops, reaching leaves unattainable by other dinosaurs. New research has challenged this view. John A. Whitlock, now at Mount Aloysius College, reconstructed feeding strategies among diplodocoids, a group of sauropods that includes the familiar *Apatosaurus* and *Diplodocus* that persisted from the Late Jurassic to the Late Cretaceous. Variation in snout shape and microscopic wear patterns on teeth indicate that some sauropods specialized in particular kinds of plants and others were generalists; whereas some grazed on ground-height plants, others fed from the trees. Different research groups have drawn similar conclusions from analyses of sauropod neck postures, which show that sauropod feeding was additionally constrained by vertebral flexibility: sauropods varied in their ability to crane their necks to reach plants up high and down low. This diversity of dining habits helps to explain how so many giants shared the same ecosystems.

Sauropod dietary adaptations flourished in the Cretaceous, concurrent with the rise of flowering plants. An old-school hypothesis held that other dinosaurian vegetarians better suited to dining on these new plants pushed sauropods to the evolutionary sidelines in the Cretaceous. In this view, sauropods, with their weak teeth, small heads and giant bodies, were no match for the more efficient duckbills and horned dinosaurs, which possessed conveyor belts of teeth packed together to form formidable dental batteries that acted as one giant, ever growing powerful tooth.

What we now know is that the Cretaceous was actually the most diverse interval of sauropod evolution and arguably the most interesting. Far from being outcompeted by newcomers, sauropods diversified in form and function, evolving novel means of exploiting a wide variety of plants. Take, for example, *Nigersaurus:* a 115-million-year-old species discovered in Niger in the mid-1990s by Paul C. Sereno of the University of Chicago and his colleagues. The creature evolved broad dental batteries with extremely fast tooth replacement rates (one new tooth in each position every month, which is up to twice as fast as those of duckbills and horned dinosaurs), keeping teeth sharp

TYLER KEILLOR

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for efficient clipping of vegetation. The orientation of the semicircular canals of the inner ear—the organs of balance—in *Nigersaurus* suggests that this animal usually held its head with its muzzle pointing directly downward, rotated far from the usual horizontal pose inferred for other sauropods. This position suggests that it specialized in feeding on plants near the ground.

As the Cretaceous progressed and flowering plants diversified, sauropods found themselves with more options on the table. Microscopic analysis of fossilized feces, or coprolites, from titanosaurs has revealed silicified plant tissues called phytoliths that document at least five different types of grass in addition to such flowering plants as magnolias, conifers and palms. This discovery, reported by Vandana Prasad of the Birbal Sahni Institute of Paleobotany in India and her colleagues in 2005, pushed the origin and diversification of modern grasses back by some 30 million years and supports the notion that some sauropods fed fairly indiscriminately. As is true for any respectable fast-growing vertebrate herbivore, it paid for sauropods to not be picky. Far from being pushed out of these emergent ecosystems, they seem to have taken full advantage of the new resources, eating everything from the tops of trees to the forage at their feet.

Enhanced oxygen intake may have further fueled sauropod growth. In living birds, air sacs connected to outpocketings of the lungs invade their hollowed-out vertebrae, allowing the birds to suck more oxygen out of each breath than mammals can. Air sacs in birds allow for a unidirectional airflow through the lungs, which increases the oxygen content extracted from each breath. (In mammals, airflow is bidirectional: each new breath mixes in our lungs with old air, resulting in a relatively inefficient method of oxygen extraction.) Sauropod vertebrae resemble those of modern birds in having nearly identical internal cavities and a complex pattern of external hollows bounded by struts. The greatest hollowness, or pneumaticity, is found in neck and trunk vertebrae, but in some sauropod species it can extend to parts of the shoulders, hips and tail. The primary effect of pneumatization is overall reduction in the weight of the vertebral column, and estimates indicate that it may have significantly reduced sauropod body mass. For example, the North American colossus *Sauroposeidon* had a neck that was more than 75 percent air. It is also possible that, as in birds, the pneumatized vertebrae of sauropods housed an extensive air sac system with flow-through ventilation of the lungs that aided respiration and would have allowed them to maintain stable, high metabolic rates and increased activity levels consistent with their rapid growth rate and massive adult body size.

WHEN THE GOING GOT TOUGH

BEING BIG had a real advantage for sauropods, as it does for modern behemoths. Even before they were halfway grown, many sauropod species exceeded the size of adult elephants, which have essentially no predators (apart from humans). Once they reached adult size, they were probably fairly immune to serious predators, such as *Allosaurus*. Large body size also left sauropods extra vulnerable in cases of food and water shortage. Yet some may have evolved solutions to even that problem: a handful of titanosaur species bore bizarre bony plates in their skin called osteoderms. A number of modern animals have osteoderms—they make up the armorlike covering of crocodilians, lizards and armadillos, and they formed the distinctive bony plates and spikes in dinosaurs such as *Stegosaurus*. Where on the sauropod body osteoderms resided has been impossible to determine, however, making it hard for scientists to discern their function.

New findings may resolve this question. In 2011 we described two osteoderms that were found in Madagascar alongside one juvenile skeleton and one adult skeleton of a titanosaur called *Rapetosaurus*. At 57 centimeters long and more than 27 centimeters thick, with a volume of nearly 10 liters, the adult specimen is the most massive osteoderm ever discovered from any backboned animal. CT scans and drill cores indicate that the osteoderms of *Rapetosaurus* hollowed out during the course of the animal's life, and at very large sizes about five liters' worth of internal bone was replaced, probably with soft tissue. Instead of the pavementlike covering of osteoderms found in living animals, *Rapetosaurus* (and probably some other titanosaurs) had only a few large plates.

These features of the *Rapetosaurus* osteoderms helped us rule out several competing ideas about the function of osteoderms in titanosaurs. Such internally hollow elements would offer little in the way of protection because they would shatter under the force of a predator's jaws. Similarly, the low surface area to volume ratio of the elements and their sparse distribution in the skin would have rendered them useless for thermoregulation. We argue that titanosaur osteoderms instead served as an invaluable mineral reserve that may have helped sustain growth rates and egg-laying ability even through the harshest times, just as they do in some modern animals. In all living vertebrates, including humans, bone mineral is sacrificed to help maintain blood calcium levels. This resorption often increases seasonally, when resources are rare, during egg laying and with increasing age—which in humans leads to osteoporosis. Osteoderms have rich blood supplies that serve as the perfect conduits for the cells that do the resorbing and for the mineral resources that are unlocked from deep inside bones. This idea makes a lot of sense for a massive sauropod in Late Cretaceous Madagascar. Back then, the island was a harsh place to live—regular, severe droughts forced meat-eating dinosaurs such as *Majungasaurus* to cannibalize members of its own species and brought about the demise of innumerable animals, from frogs and birds to sauropods. Osteoderms may have helped sauropods in Madagascar and elsewhere survive environmental perturbations, including frequent, intense droughts.

Sauropods seem to test the laws of biological possibility in how fast they grew and how large they became. These breaches could have painted them into an evolutionary corner, yet our growing knowledge of the fossil record suggests the opposite. Indeed, they went extinct, but before that inescapable disaster struck, sauropods had a spectacular 150-million-year run as one of the most remarkable extravagances that evolution has ever invented. SA

Kristina A. Curry Rogers is a vertebrate paleontologist at Macalester College. Her research centers on the evolution and paleobiology of sauropods. She has traveled the world—from Argentina to Zimbabwe—in search of dinosaur fossils. **Michael D. D'Emic** is a vertebrate paleontologist at Stony Brook University. His fieldwork focuses on Early Cretaceous sauropods from Montana and Wyoming. He is particularly interested in a group of sauropods known as titanosaurs.

MORE TO EXPLORE

The Sauropods: Evolution and Paleobiology. Kristina A. Curry Rogers and Jeffrey A. Wilson. University of California Press, 2005.

Inferences of Diplodocoid (Sauropoda: Dinosauria) Feeding Behavior from Snout Shape and Microwear Analyses. John A. Whitlock in *PLOS ONE*, Vol. 6, No. 4, Article No. e18304; April 6, 2011.

Sauropod Dinosaur Osteoderms from the Late Cretaceous of Madagascar. Kristina Curry Rogers et al. in *Nature Communications*, Vol. 2, Article No. 564. Published online November 29, 2011.

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DINING OUT: A herd of *Kosmoceratops* dinosaurs grazes among the cypress trees 76 million years ago in a primeval swamp in what is now southern Utah.

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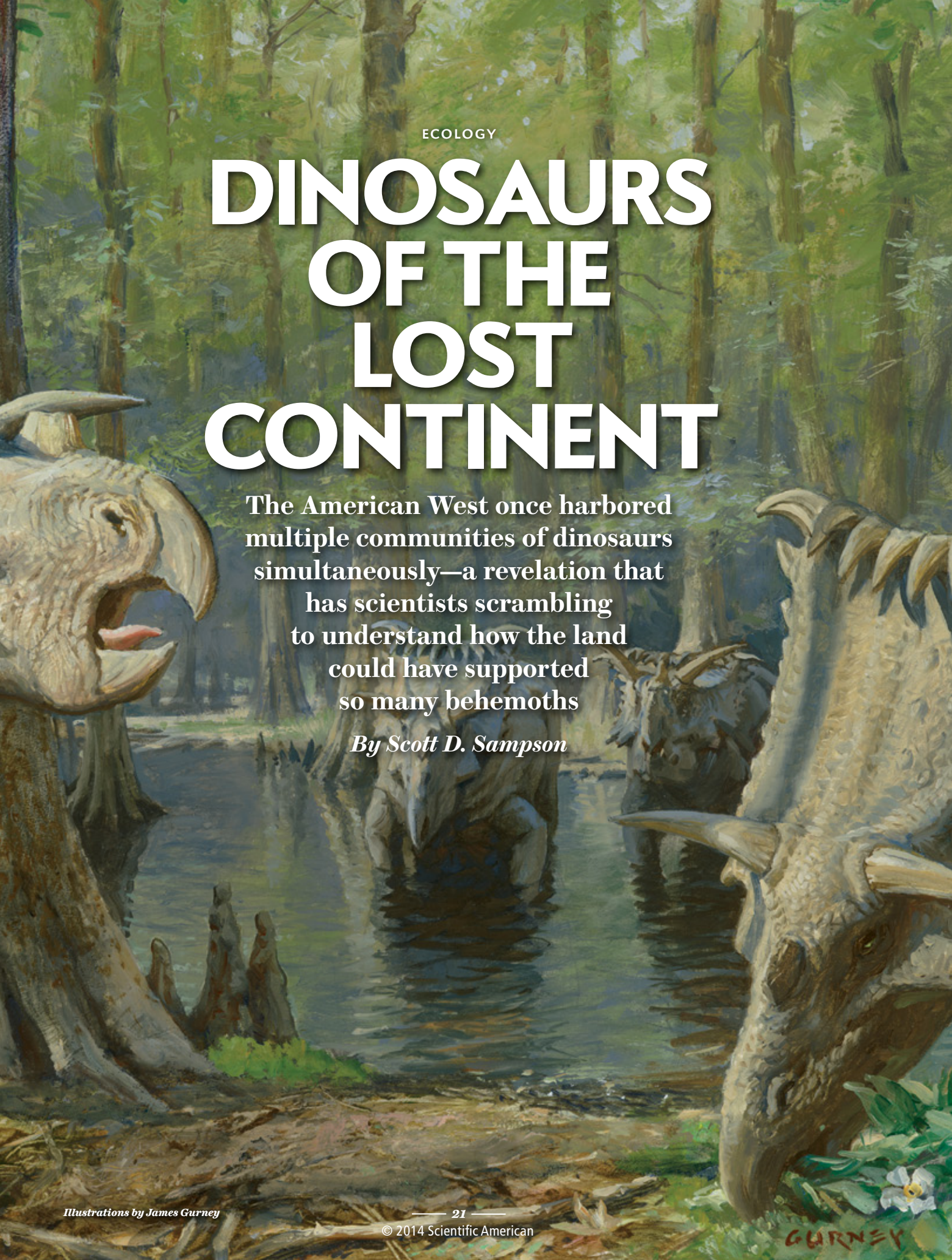
ECOLOGY

DINOSAURS OF THE LOST CONTINENT

The American West once harbored multiple communities of dinosaurs simultaneously—a revelation that has scientists scrambling to understand how the land could have supported so many behemoths

By Scott D. Sampson



Illustrations by James Gurney

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ON A COOL SEPTEMBER MORNING IN 2010 MY CREW AND I BEGAN OUR DAILY DESCENT from camp back into deep time, walking single file down a steep, knife-edge ridge of sandstone and mudstone in southern Utah's Grand Staircase-Escalante National Monument. Each of us carried water, a field notebook, lunch, a rock hammer and other hand tools. Heavier tools and materials—rock saws, picks, shovels, bags of plaster and swaths of burlap—awaited us half a mile away at the dig site. Even from the hilltop we could easily see the plaster jackets down in the quarry—alabaster beacons in a wilderness of arid, gray-striped badlands. Some of the irregular lumps were not much bigger than a loaf of bread. Others spanned 10 feet and tipped the scales at more than a ton. All contained the bony remains of animals that coexisted here 76 million years ago.

Over the course of two field seasons this single quarry—one of many in the fossil-rich rocks of the Kaiparowits Formation—had yielded a striking array of creatures, including several dinosaurs. Most impressive was a largely complete skeleton of *Gryposaurus,* a massive, duck-billed plant eater approaching the size of *Tyrannosaurus.* The crew was now under pressure to finish excavating the remaining fossils before the helicopter came in a few days to airlift the priceless cargo to a nearby road. From there the fossils would travel by truck to the Natural History Museum of Utah in Salt Lake City, where trained volunteers would painstakingly open the jackets, remove the rock and glue the bones back together over a period of months.

Pausing on a sandstone ledge to soak in the sprawling vista below, I imagined for the umpteenth time how this place might have appeared when these dinosaurs roamed. Back then, much of the territory was an immense, waterlogged floodplain. Sluggish rivers from mountains to the west meandered across a verdant landscape interspersed with ponds and lakes. Cypress trees thrived in the swampy lowlands; better-drained settings supported forests of conifers and flowering trees. Vines draped the tree branches, and the buzzing of insects filled the humid air. The scene would have called to mind the swamplands of northern Louisiana today—but with the addition of more than a dozen dinosaur species, from herbivorous duck-billed hadrosaurs and horned dinosaurs (called ceratopsids) to carnivorous, sickle-clawed dromaeosaurs and a type of giant tyrannosaur.

Our excavations in this remote region over the past 14 years—a joint project of the Utah museum, the U.S. Bureau of Land Management, and the Denver Museum of Nature & Science—have opened a fascinating window on the mix of dinosaur species that lived during the so-called Campanian Stage of the Late Cretaceous period, between 83.5 million and 70.6 million years ago, a time when dinosaurs here were undergoing perhaps their greatest florescence.

IN BRIEF

Between 90 million and 70 million years ago, during the Late Cretaceous period, a shallow sea flooded the central region of North America, subdividing the continent into eastern and western landmasses. Scientists refer to the western landmass as Laramidia.

In the 1980s a researcher proposed that distinct dinosaur communities inhabited the northern and southern regions of Laramidia for several million years. Critics doubted that so many large animals could have shared this relatively small chunk of land, however.

But over the past decade discoveries in southern Utah have bolstered the notion of distinct dinosaur communities in the north and south, revealing a host of species new to science—including many giant varieties.

Exactly what enabled so many behemoths to coexist in such a small area remains unclear, but it may be that dinosaurs had lower energy requirements than today's large terrestrial animals do or that plants during the Late Cretaceous provided more food than their modern-day counterparts.

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UPHILL CLIMB: Members of the author's team scale a ridge out of the Kaiparowits badlands in Utah's Grand Staircase-Escalante National Monument (*1*), where they have discovered remains of a number of new dinosaur species. Fossils such as this skull of ***Kosmoceratops*** are brought to the Natural History Museum of Utah, where volunteers clean and reassemble them (*2*). Species found in that area include another horned dinosaur, ***Utahceratops*** (*3*).

RICK WICKER *Denver Museum of Nature & Science (1);*
COURTESY OF MARK LOEWEN *Natural History Museum of Utah (2 and 3)*

In a sense, the Kaiparowits fossil assemblage is unremarkable, preserving the same broad dinosaur groups unearthed from sediments of similar antiquity farther north in Montana and in Alberta, Canada. Yet the particular species in the Kaiparowits are unique, with many large-bodied forms—findings that are forcing us to reconsider much of what we thought we knew about dinosaur evolution and ecology. Let me explain.

SOUTH VS. NORTH

DURING THE LATE CRETACEOUS the earth was a hothouse world. The planet's polar regions were free of ice caps, and global sea levels tended to be exceptionally high. A warm, saltwater sea, the Western Interior Seaway, inundated the central region of North America, connecting the Arctic Ocean with the Gulf of Mexico and dividing the continent into eastern and western portions: Appalachia and Lara-

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midia, respectively. The dinosaurs, plants and other organisms we have been recovering from the Kaiparowits lived on Laramidia, a landmass less than one fifth of the size of its parent continent.

Beginning in the 1960s, fossil hunters working in the Western Interior began to notice that Late Cretaceous dinosaurs found in Montana and Alberta belonged to distinct species from those recovered from similarly aged rocks farther south in such places as New Mexico and Texas. In the 1980s Thomas Lehman of Texas Tech University tabulated the geographical occurrences of dinosaurs and other vertebrate creatures on Laramidia and found evidence of distinct northern and southern assemblages during the final 15 million years of the Cretaceous period, including the Campanian Stage. Lacking any indication of a physical barrier to north-south dispersal, Lehman hypothesized that a latitudinal climate gradient had produced distinct communities of plants and animals, including a bevy of big-bodied dinosaurs. His was a bold theory. Other researchers questioned the likelihood of multiple dinosaur communities coexisting on the diminutive landmass of Laramidia. It simply did not seem possible that so many kinds of giants could have shared such a small chunk of real estate.

Critics of Lehman's hypothesis pointed out that any apparent provincialism might be illusory, the result of uneven sampling of fossils through time. Given that the Late Cretaceous spans many millions of years, they noted, perhaps paleontologists working at different latitudes in the Western Interior have effectively been "time traveling" to different intervals. If so, this imbalanced sampling through time could generate the perception of distinct, coeval faunal provinces even if only a single cosmopolitan dinosaur fauna existed on Laramidia at any given geologic moment. Alternatively, skeptics observed, the seemingly distinct dinosaur communities could be the result of poor geographical sampling. Until recently, the vast majority of Laramidian dinosaurs were known from the north, particularly Alberta and Montana. Perhaps a more thorough sampling of dinosaurs from southern Laramidia would ultimately reveal a single, widespread community. These issues remained unresolved when my colleagues and I began our work in southern Utah in 2000.

The fossils that we have recovered from Grand Staircase-Escalante go a long way toward filling the southern dinosaur gap on Laramidia and bolstering Lehman's theory. Dating of the fossils has been essential to answering the question of whether distinct, coeval dinosaur provinces existed in the north and south. Team geologist Eric M. Roberts of James Cook University in Australia found layers of volcanic ash scattered throughout the Kaiparowits strata that he was able to date using radiometric techniques. The results indicated that the key, fossil-rich hot zone formed over a period of one million years between 76.5 million and 75.5 million years ago. Comparing these ash dates with those from other Laramidian formations revealed that the Kaiparowits Formation closely overlapped in time with the Dinosaur Park Formation in Alberta. We now had strong evidence that at least one pair of northern and southern dinosaur assemblages lived concurrently.

The next step was to assess whether the dinosaurs themselves differed from north to south. Of the 17 dinosaur varieties that the team has recovered so far from the one-million-year interval, 13 are sufficiently complete to allow species-level identifications. Only one—a duck-billed hadrosaur in the *Gryposaurus* genus—was possibly present farther north. This species looks very similar to *Gryposaurus notabilis* from Alberta, but the identification is currently uncertain, and investigations are under way to assess whether ours is a distinct species.

Outside of this single question mark, the emergent picture is clear. Every other Kaiparowits dinosaur species thus far identified differs from those found farther north. When small to midsize carnivores such as the oviraptorosaur *Hagryphus* and the troodont *Talos* prowled ancient Utah, the same groups were represented instead by *Chirostenotes* and *Troodon,* respectively, up in Alberta. Similarly, whereas a large-bodied, short-faced tyrannosaur named *Teratophoneus* was the top land carnivore in the Utah region, other tyrannosaurs such as *Gorgosaurus* filled this role in the north. Plant-eating dinosaurs in the Kaiparowits Formation are similarly distinct from the northern forms. One of these is *Parasaurolophus,* a bizarre hadrosaur with a long, tubular crest on the top of its head. Three species of *Parasaurolophus* have been found previously, one in Alberta and two in New Mexico; the Utah species appears to be new to science.

The pattern repeats among the ceratopsids. One species that we dubbed *Utahceratops* has a long-frilled skull approaching seven feet in length. The skull of a second, shorter-frilled species, *Kosmoceratops,* is ornate in the extreme, bearing 15 horns on its head, the most of any dinosaur. While *Utahceratops, Kosmoceratops* and a third ceratopsid dinosaur, *Nasutoceratops,* foraged in Utah, different species of horned dinosaurs munched on plants up north.

The newly discovered Kaiparowits dinosaur assemblage in Grand Staircase-Escalante provides by far the strongest evidence of isolated dinosaur provinces on Laramidia. Although the same major groupings of dinosaurs occurred in both the north and south, northerners and southerners were distinct species. None of the more than 50 Campanian dinosaur species from numerous formations can yet be confidently placed in both the north and south. These findings effectively refute the possibility that distinct northern and southern assemblages are merely an artifact of incomplete temporal or geographical sampling. Instead we must come to grips with the fact that at least two dinosaur communities coexisted on this landmass for about a million years of late Campanian time.

LAND OF GIANTS

THAT MANY OF THE DINOSAURS in these two communities were giants deepens the Laramidia mystery. Studies of modern-day terrestrial mammals show a tight connection between maximal body size and land area. Large-bodied forms tend to range farther, both as individuals and as species, because bigger animals require more area to obtain enough food. For the same reason, species with more extensive home ranges tend to have lower population densities. Maximum body size in giant terrestrial mammal species, then, reflects a balance between maintaining population densities low enough to avoid overexploitation of food resources yet high enough to avoid extinction. Ultimately the upper limits of both body size and species diversity among megavertebrates are constrained by a combination of physiology (higher metabolic rates demand greater food intake), food availability and landmass area, with more extensive landmass areas typically supporting more kinds of large-bodied species. This relation places the severest demands on big-bodied carnivores, which must maintain relatively larger home ranges than herbivores because only a small fraction of an ecosystem's total energy budget reaches the top of the food chain.

In theory, giant dinosaurs should have followed a pattern similar to that of today's large terrestrial mammals, with few species on the

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FINDINGS

Dinosaur Diversity

Between about 90 million and 70 million years ago, during the Late Cretaceous, an interior sea isolated the western portion of what is now North America, turning that strip into a landmass called Laramidia. Researchers have long observed that northern and southern Laramidia seem to have hosted different communities of dinosaurs and other animals. But critics questioned whether the pattern might instead be the result of uneven sampling of fossils over time and space. Recently discovered fossils in the Kaiparowits Formation of Grand Staircase-Escalante National Monument have revealed a previously unknown assemblage of dinosaur species that lived at the same time as a different assemblage farther north, bolstering the theory of distinct northern and southern dinosaur provinces in Laramidia. The nature of the barrier that separated these northern and southern dinosaurs remains a mystery. The map below shows some of the horned dinosaurs (as represented by their skulls) from these northern and southern assemblages.

GEORGE RETSECK (*map*); ADAPTED FROM RON BLAKEY *Northern Arizona University*

relatively small Laramidian landmass. Yet taken together, the animal communities represented in the Kaiparowits Formation and the Dinosaur Park Formation contain at least 17 to 20 coeval species of giant dinosaurs—that is, forms exceeding one ton in adult body mass—with most weighing in at more than two tons. By modern standards, that scenario seems downright bizarre. Today the only place on earth where you can find an abundance of giants is Africa, which harbors six mammals with a mean body mass in excess of one ton, all of them herbivores: the giraffe, the hippopotamus (which spends most of its time in freshwater rather than on land), and two species each of elephants and rhinoceroses.

It is true that Africa and some other landmasses housed considerably more large terrestrial species in the past. For example, during the Early Pleistocene, between about 2.5 million and two million

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years ago, Africa supported on the order of 16 megaherbivore mammals: multiple varieties of giraffes, elephants, hippos and rhinos, plus several types of big-bodied antelope that weighed nearly a ton. Nevertheless, a number of lines of evidence indicate that the Laramidian dinosaur example is exceptional.

First, Laramidia was less than one fifth of the size of Pleistocene Africa, so those 17 to 20 dinosaur behemoths were confined to a much smaller area than their mammalian counterparts. Furthermore, abundant evidence from mass death accumulations, or bone beds, indicates that many species of hadrosaurs and ceratopsids congregated for at least part of every year in large "herds," numbering in the hundreds (and perhaps thousands) of animals. Second, mammal-dominated ecosystems from the Pleistocene onward have few terrestrial carnivores approaching a ton. Indeed, mammal evolution on land has yet to produce carnivores that even approach the magnitude of a tyrannosaur. Africa's largest predator, the lion, typically weighs less than 600 pounds; Laramidia, in contrast, was home to at least three giant tyrannosaurs, all of which apparently exceeded a ton. Third, whereas paleontologists have found Early Pleistocene fossils in multiple African countries, current sampling on Laramidia is limited to two coeval geologic formations. Given that Laramidian dinosaurs appear to have had considerably smaller species ranges than modern terrestrial mammals, with minimal overlap between concurrent communities, it seems highly probable that additional dinosaurs lived on this landmass during the Campanian. If so, the total number of contemporaneous giants on Laramidia may have far

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KILLER INSTINCT: ***Teratophoneus,*** **a type of tyrannosaur, takes down a duck-billed hadrosaur called** ***Gryposaurus.*** **Remains of both types of dinosaurs have been recovered from deposits in Grand Staircase-Escalante National Monument dating to about 76 million years ago.**

surpassed 20 species. In short, the new Kaiparowits evidence strongly suggests that dinosaurs exceeded known mammalian limits for species richness at large body sizes.

CONSERVATIVE DINOS OR PRODUCTIVE PLANTS?

THIS COMPARISON between African mammal giants and Laramidian dinosaur giants brings us back to the burning question elicited by Lehman's hypothesis. How did dinosaurs manage to squeeze so many varieties of giants into such a small area? Either these dinosaurs got by on less food than modern giants do, or the environments they inhabited produced more food than we see in modern settings.

Scientists have long debated whether dinosaur metabolism was more like that of the cold-blooded ectotherms (such as amphibians and reptiles) or the warm-blooded endotherms (such as birds and mammals). If their metabolic rates were intermediate between these groups, causing them to have lower energy requirements than large mammals do, this difference could help explain how so many big-bodied species coexisted on the relatively tiny landmass of Laramidia. Recent research by Brian K. McNab of the University of Florida supports this notion of "Goldilocks" dinosaurs—not cold-blooded, not hot-blooded, but something in between. McNab has found a range of evidence indicating that lower energy expenditures of dinosaurs may have enabled their communities to support biomasses up to five times greater than those of mammalian herbivores in present-day Africa.

Alternatively, relative to present-day land ecosystems, Late Cretaceous plants may have offered megaherbivores foods that were more abundant or more nutritious, or both. Plant diversity and abundance are controlled by such factors as precipitation, temperature, length of growing season and availability of niches. Today the greatest diversity and biomass of plants tend to occur in the tropics, but during the hothouse of the Late Cretaceous high temperatures may have limited plant and animal diversity in the equatorial regions. At midlatitudes such as those occupied by much of Laramidia, in contrast, the climate was mild and the growing season long. To the west, Laramidian mountain ranges and rivers multiplied the number of available niches. To the east, the Western Interior Seaway ameliorated temperatures while providing a major source of precipitation. Paleobotanist Ian Miller of the Denver Museum of Nature & Science has thus far recovered more than 100 different plant varieties from the Kaiparowits strata. Although much more work needs to be done, all indicators suggest that the dinosaur communities in Laramidia were founded on a great bounty and diversity of plants.

Figuring out whether slower metabolic rates or augmented food supplies enabled dinosaurs to reach such gargantuan proportions and high richness of species will require further testing. My hunch is that both factors were involved. One thing we can say with confidence is that the hothouse world of the dinosaurs was very different from the world of today. Many of the major biomes of our present-day icehouse earth—for example, grasslands, tundra and rain forests—were absent during the dinosaurs' reign, and we are still trying to glean even a basic understanding of their hothouse predecessors. The good news is that paleontology is becoming increasingly interdisciplinary—involving collaborations with geologists, paleoecologists and paleoclimatologists, to name a few—increasing the odds that fruitful insights will emerge.

Meanwhile our work in the Kaiparowits Formation, like any scientific research worth its salt, is generating as many questions as answers. How many distinct dinosaur communities existed at any one time on the lost continent of Laramidia? What was the nature of the barrier separating the northern and southern communities? Was this boundary based solely on climatic variation between the north and south, as first thought? Or, as some geologists now suspect, was some kind of physical barrier present, perhaps a series of large rivers flowing from the mountains to the sea at the latitude of northern Utah and Colorado?

One final, intriguing implication is worth noting. If it turns out that dinosaurs tended toward much smaller species ranges than equivalent-size mammals, the richness of dinosaur species globally may have been far greater than previously anticipated. Which is to say that many, many more weird and wonderful dinosaurs are probably still buried out there, patiently awaiting discovery. SA

Scott D. Sampson is vice president of research and collections and chief curator at the Denver Museum of Nature & Science. He has been leading efforts to recover Late Cretaceous fossils from Grand Staircase-Escalante National Monument in Utah since 2000. He is also the scientific adviser for and on-air host of the PBS KIDS television series *Dinosaur Train*.

MORE TO EXPLORE

Dinosaurs, Dragons, and Dwarfs: The Evolution of Maximal Body Size. Gary P. Burness, Jared Diamond and Timothy Flannery in *Proceedings of the National Academy of Sciences USA,* Vol. 98, No. 25, pages 14518–14523; December 4, 2001.

Resources and Energetics Determined Dinosaur Maximal Size. Bruce K. McNab in *Proceedings of the National Academy of Sciences USA,* Vol. 106, No. 29, pages 12184–12188; July 21, 2009.

Dinosaur Odyssey: Fossil Threads in the Web of Life. Scott D. Sampson. University of California Press, 2009.

New Horned Dinosaurs from Utah Provide Evidence for Intracontinental Dinosaur Endemism. Scott D. Sampson et al. in *PLOS ONE,* Vol. 5, No. 9; September 22, 2010.

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ROCKY HILLSIDE
entombs some of Madagascar's oldest fossils of land vertebrates.

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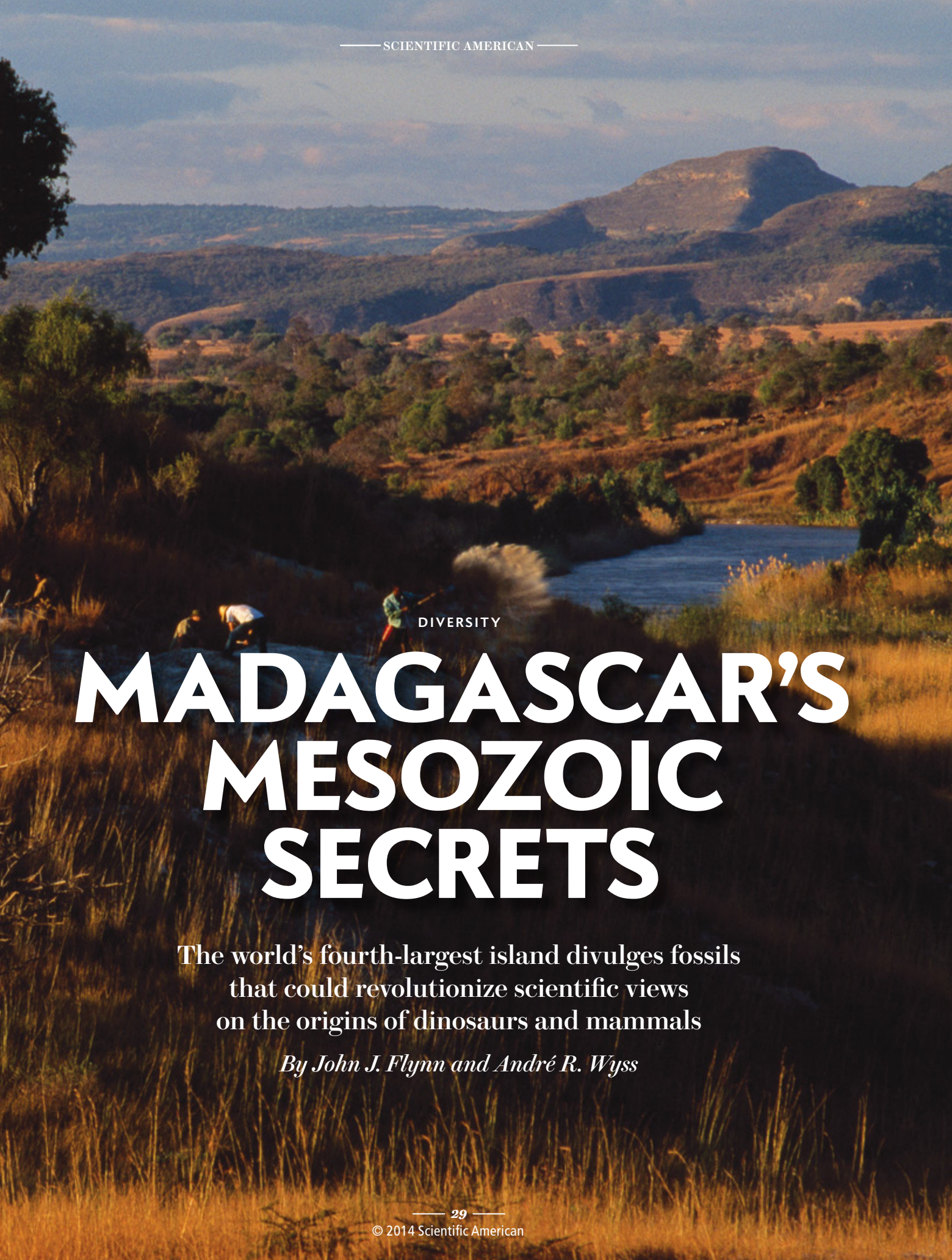

DIVERSITY

MADAGASCAR'S MESOZOIC SECRETS

The world's fourth-largest island divulges fossils that could revolutionize scientific views on the origins of dinosaurs and mammals

By John J. Flynn and André R. Wyss

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THREE WEEKS INTO OUR FIRST FOSSIL-HUNTING EXPEDITION IN MADAGASCAR IN 1996, we were beginning to worry that dust-choked laundry might be all we would have to show for our efforts. We had turned up only a few random teeth and bones—rough terrain and other logistical difficulties had encumbered our search. With our field season drawing rapidly to a close, we finally stumbled on an encouraging clue in the southwestern part of the island. A tourist map hanging in the visitor center of Isalo National Park marked a local site called "the place of animal bones." We asked two young men from a neighboring village to take us there right away.

Our high hopes faded quickly as we realized that the bleached scraps of skeletons eroding out of the hillside belonged to cattle and other modern-day animals. This site, though potentially interesting to archaeologists, held no promise of harboring the much more ancient quarry we were after. Later that day another guide, accompanied by two dozen curious children from the village, led us to a second embankment similarly strewn with bones. With great excitement we spotted two thumb-sized jaw fragments that were undoubtedly ancient. They belonged to long-extinct, parrot-beaked cousins of the dinosaurs called rhynchosaurs.

The rhynchosaur bones turned out to be a harbinger of a spectacular slew of prehistoric discoveries. Since then, the world's fourth-largest island has become a prolific source of new information about animals that walked the land during the Mesozoic era, from 252 million to 66 million years ago, when both dinosaurs and mammals were making their debut. We unearthed the bones of what seemed like primitive dinosaurs, which we suspected were older than any found previously. We have also stirred up controversy with the discovery of a shrewlike creature that seems to defy a prominent theory of mammalian history by being in the "wrong" hemisphere. These specimens, and others collected over five field seasons, enabled us to begin painting a picture of ancient Madagascar and shaped our strategy for a sixth expedition in 2003.

Much of our research over the past three decades has been aimed at unraveling the history of land-dwelling animals on the southern continents. Such questions have driven other paleontologists to fossil-rich locales in South Africa, Brazil, Antarctica and India. Rather than probing those established sites for additional finds, we were lured to Madagascar: the island embraces vast swaths of Mesozoic-age rocks, but until recently only a handful of terrestrial vertebrate fossils from that time had been discovered there. Why? We had a hunch that no one had looked persistently enough to find them.

Persistence became our motto as we launched our 1996 expedition. Our team consisted of a dozen scientists and students from the U.S. and the University of Antananarivo in Madagascar. In addition to scientific and educational benefits, our partnership with the country's leading university facilitated the acquisition of collecting and exporting permits—requisite components of all paleontological fieldwork. Before long, however, we ran into logistical obstacles that surely contributed to earlier failures to find ancient fossils on the island. Mesozoic deposits in western Madagascar are spread over an area roughly the size of California. Generations of oxcarts and foot travel have carved the only trails into remote areas, and most of them are impassable by even the brawniest four-wheel-drive vehicles. We had to haul most of our food, including hundreds of pounds of rice, beans and canned meats, from the capital. Fuel shortages sometimes seri-

IN BRIEF

In Madagascar's sedimentary record, the authors' team unearthed what at first seemed to be the remains of dinosaurs but turned out to be those of an ancient, previously unknown reptile species. **Its teeth** and part of its skull resemble those of prosauropod dinosaurs—precursors of the giant, long-necked sauropods—and suggest that some features thought to be characteristic of dinosaurs might have debuted earlier than previously thought.

The team also found fossils of evolutionary cousins of mammals that may have arisen millions of years earlier than assumed.

PRECEDING PAGES: MARIA STENZEL *National Geographic Image Collection*

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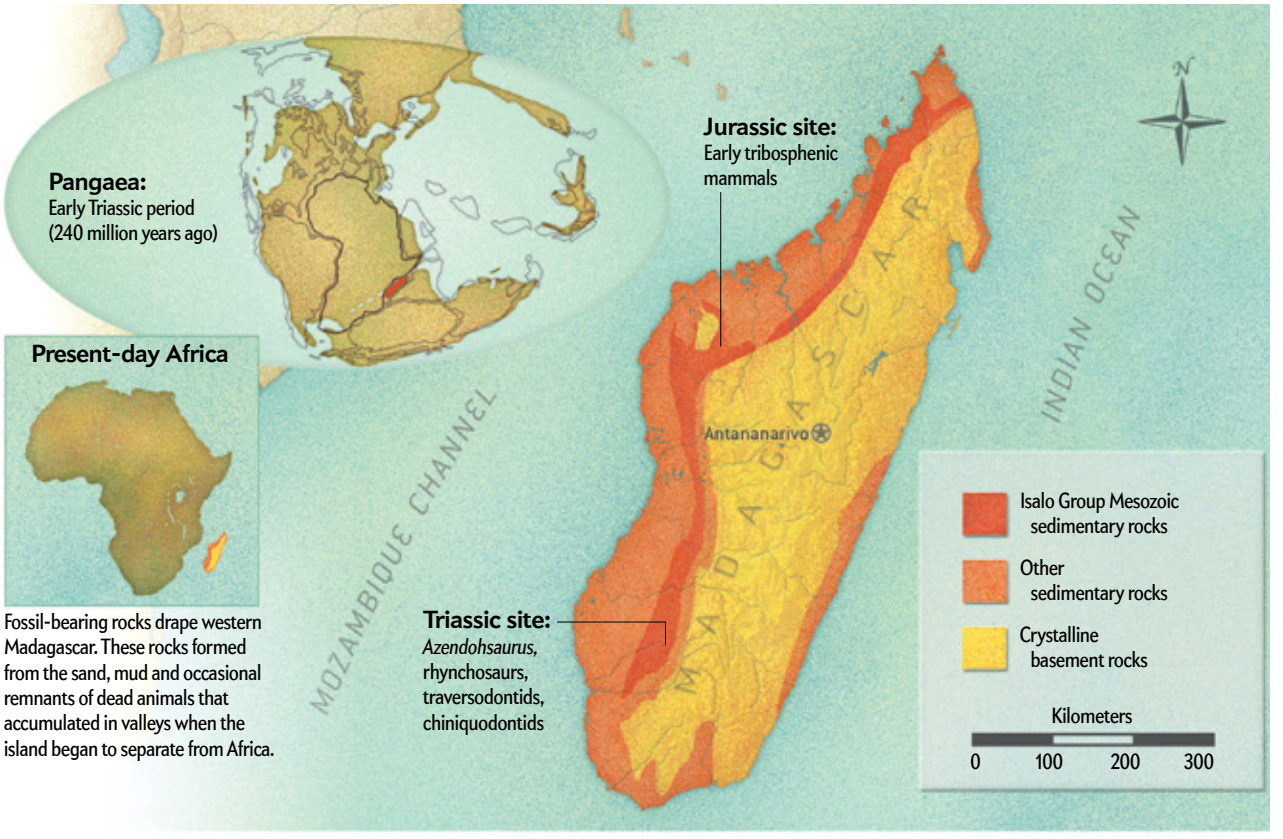
MAPS

Madagascar Then and Now



ously restricted mobility, and our work was even thwarted by wildfires, which occur frequently and rage unchecked. New challenges arose unexpectedly, requiring us to adjust our plans on the spot.

ANCIENT LUCK

PERHAPS THE MOST DAUNTING obstacle we faced in prospecting such a large region was deciding where to begin. Fortunately, we were not planning our search blindly. The pioneering fieldwork of geologists such as Henri Besairie, who directed Madagascar's ministry of mines during the mid-1900s, provided us with large-scale maps of the island's Mesozoic rocks. From those studies we knew that a fortuitous combination of geologic factors had led to the accumulation of a thick blanket of sediments over most of Madagascar's western lowlands—and gave us good reason to believe that ancient bones and teeth might have been trapped and preserved there.

At the dawn of the Mesozoic era 252 million years ago, it would have been possible to walk from Madagascar to almost anywhere else in the world. All of the planet's landmasses were united in the supercontinent Pangaea, and Madagascar was nestled between the western coast of what is now India and the eastern coast of present-day Africa [*see map above*]. The world was much warmer than at present—even the poles were free of ice. In the supercontinent's southern region, Gondwana, enormous rivers coursed into lowland basins that would eventually become the Mozambique Channel, which today spans the 250 miles between Madagascar and eastern Africa.

These giant basins represent the edge of the geologic gash created as Madagascar began pulling away from Africa more than 240 million years ago. This seemingly destructive process, called rifting, is an extremely effective way to accumulate fossils. (Indeed, many of the world's most important fossil vertebrate localities occur in ancient rift settings.) The rivers flowing into the basins carried with them mud, sand, and occasionally the carcasses or bones of dead animals. Over time the rivers deposited this material as a sequence of vast layers. Continued rifting and the growing mass of sediment caused the floors of the basins to sink ever deeper. This depositional process persisted for nearly 100 million years, until the basin floors thinned to the breaking point and molten rock ascended from the planet's interior to fill the gap as new ocean crust.

Up to that point nature had afforded Madagascar three crucial ingredients required for fossil preservation: dead organisms, holes in which to bury them (rift basins), and material to cover them (sand and mud). But special conditions were also needed to ensure that the fossils were not destroyed before they could be found millions of years later. Again, geologic circumstances proved fortuitous. As the newly separated landmasses of Africa and Madagascar drifted farther apart, their sediment-laden coastlines rarely experienced volcanic eruptions or other events that could have destroyed buried fossils. Also key for fossil preservation is that the ancient rift basins ended up on the western side of the island, which today is dotted with dry forests, grasslands and desert scrub. In a more humid environment, such deposits

SARA CHEN

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Tiny Bones to Pick

Paleontologists brave wildfires, parasites and scorching temperatures in search of ancient mammal fossils

The three Land Rovers pause while John Flynn consults the device in his hand. "Is the GPS happy?" someone asks him. Flynn concludes that it is, and the caravan continues slowly through the bush, negotiating trails usually traversed by oxcart. We have been driving since seven this morning, when we left Madagascar's capital city, Antananarivo. Now, with the afternoon's azure sky melting into pink and mauve, the group is anxious to locate a suitable campsite. A small cluster of thatched huts comes into view, and Flynn sends an ambassador party on foot to ask the inhabitants whether we may camp in the area. By the time we reach the nearby clearing, the day's last light has disappeared, and we pitch our tents in the dark. Tomorrow the real work begins.

The expedition team of seven Malagasies and six Americans, led in 2000 by paleontologists Flynn and André Wyss, now at the American Museum of Natural History in New York City and the University of California, Santa Barbara, respectively, has come to this remote part of northwestern Madagascar in search of fossils belonging to early mammals. Previous prospecting in the region had revealed red and buff-colored sediments dating back to the Jurassic period—the ancient span of time (roughly 201 million to 145 million years ago) during which mammals made their debut. Among the fossils unearthed was a tiny jaw fragment with big implications.

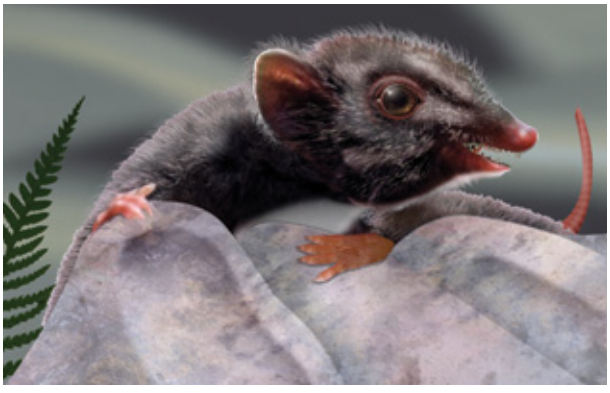
Conventional wisdom holds that the precursors of modern placental and marsupial mammals arose toward the end of the Jurassic in the Northern Hemisphere, based on the ages and locations of the earliest remains of these shrewlike creatures, which are characterized by so-called tribosphenic molars. But the Malagasy jaw, which Flynn and Wyss have attributed to a new genus and species, *Ambondro mahabo*, possesses tribosphenic teeth and dates back some 167 million years to the Middle Jurassic. As such, their fossil suggests that tribosphenic mammals arose at least 25 million years earlier than previously thought and possibly in the south rather than the north.

No one has disputed the age of *A. mahabo*, but not everyone agrees that the finding indicates that tribosphenic mammals originated in the south. Fossil mammal expert Zhe-Xi Luo, now at the University of Chicago, and several of his colleagues have suggested that *A. mahabo* and a similarly surprising fossil beast from Australia named *Ausktribosphenos nyktos* might instead represent a second line of tribosphenic mammals—one that gave rise to the egg-laying monotremes. But Flynn and Wyss counter that some of the features that those researchers use to link the southern tribosphenic mammals to monotremes may be primitive resemblances and therefore not indicative of an especially close evolutionary relationship.

As with so many other debates in paleontology, much of the controversy over when and where these mammal groups first appeared stems from the fact that so few ancient bones have ever been found. With luck, this season's fieldwork will help fill in gaps in the fossil record. And recovering more specimens of *A. mahabo* or remains of previously unknown mammals could bolster considerably Flynn and Wyss's case for a single, southern origin for the ancestors of modern placentals and marsupials.

The next morning, after a quick breakfast of bread, peanut butter and coffee, we are back in the vehicles, following the GPS's trail of electronic bread crumbs across the grassland to a fossil locality the team found at the end of its previous expedition. Stands of doum palms and thorny Mokonazy trees dot the landscape, which the dry season has left largely parched. By the time we reach our destination, the morning's pleasant coolness has given way to a rather toastier temperature. "When the wind stops, it cooks," remarks William Simpson, a collections manager for the Field Museum, coating his face with sunscreen. Indeed, noontime temperatures often exceed 90 humid degrees Fahrenheit.

Flynn instructs the group to start at the base of the hillside and work up. Meanwhile he and



FOUR-INCH-LONG MAMMAL ***Ambondro mahabo*** **lived in Madagascar about 167 million years ago.**

FRANK IPPOLITO

would have eroded away or would be hidden under dense vegetation like the kind that hugs much of the island's eastern coast.

Initially Madagascar remained attached to the other Gondwanan landmasses: India, Australia, Antarctica and South America. It did not attain islandhood until it split from India about 90 million years ago. Sometime since then, the island acquired its suite of bizarre modern creatures, of which lemurs are the best known. For more than a century, researchers have wondered how long these modern creatures and their ancestors have inhabited the island. Illuminating discoveries by another team of paleontologists indicate that almost all major groups of living vertebrates arrived on Madagascar since sometime near the end of the Mesozoic era 66 million years ago [*see box on page 36*]. Our own probing has focused on a more ancient interval of Madagascar's history—the first two periods of the Mesozoic era.

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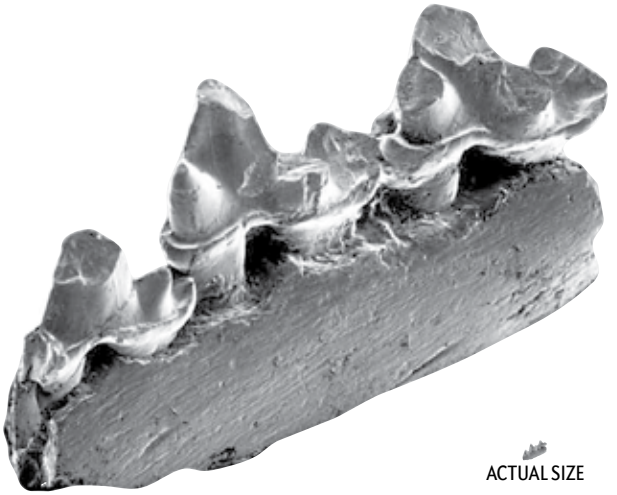
Wyss will survey the surrounding area, looking for additional exposures of the fossil-bearing horizon. "If it's something interesting, come back and get me," he calls. Awls in hand and eyes inches from the ground, the workers begin to scour the gravel-strewn surface for small bones, clues that delicate mammal fossils are preserved below. They crawl and slither in pursuit of their quarry, stopping only to swig water from sun-warmed bottles.

Because early mammal remains are so minute (*A. mahabo*'s jaw fragment, for example, measures a mere 3.6 millimeters in length), such sleuthing rarely leads to instant gratification. Rather the team collects sediments likely to contain such fossils and ships that material back to the U.S. for closer inspection. Within a few hours, a Lilliputian vertebra and femur fragment turn up—the first indications that the fossil hunters have hit pay dirt. "It's a big Easter egg hunt," Wyss quips. "The eggs are hidden pretty well, but we know they're out there."

By the third day the crew has identified a number of promising sites and bagged nearly a ton of sediment for screen washing. Members head for a dammed-up stream that locals use to water their animals. Despite the scorching heat, those working in the water must don heavy rubber boots and gloves to protect against the parasites that probably populate the murky green pool. They spend the next few hours sifting the sediments through screen-bottomed baskets and buckets. Wyss spreads the resulting concentrate on a big blue plastic tarp to dry. Volunteers at the Field Museum will eventually look for fossils in this concentrate under a microscope, one spoonful at a time, but Wyss has a good feeling about the washed remains already. "You can actually see bone in the mix," he observes. The haul that yielded *A. mahabo,* in contrast, offered no such hints to the naked eye.



JURASSIC-AGE jaw fragment of *A. mahabo* features specialized molars that are unique to tribosphenic mammals.

JOHN J. FLYNN AND SUSANA MAGALLON *The Field Museum*

Hot and weary from the screen washing, the researchers eagerly break for lunch. Under the shade of a Mokonazy tree, they munch their sardine, Gouda and jalapeño sandwiches, joking about the bread, which, four days after leaving its bakery in Antananarivo, has turned rather tough. Wyss ceremoniously deposits a ration of jelly beans into each pair of upturned palms. Some pocket the treats for later, others trade for favorite flavors, and a few ruefully relinquish their sweets, having lost friendly wagers made earlier.

Usually lunch is followed by a short repose, but today nature has a surprise in store. A brushfire that had been burning off in the distance several hours ago is now moving rapidly toward us from the northeast, propelled by an energetic wind. The crackling sound of flames licking bone-dry grass crescendos, and ashen leaf remnants drift down around us. We look on, spellbound, as cattle egrets collect in the fire's wake to feast on toasted insects, and birds of prey circle overhead to watch for rodents flushed out by the flames. Only the stream separates us from the blaze, but reluctant to abandon the screen washing, Flynn and Wyss decide to wait it out. Such fires plague Madagascar. Often set by farmers to encourage new grass growth, they sometimes spread out of control, especially in the tinderbox regions of the northwest. Indeed, the explorers will face other fires that season, including one that nearly consumes their campsite.

An hour later the flames have subsided, and the team returns to the stream to finish the screening quickly. Banks once thick with dry grass now appear naked and charred. Worried that the winds might pick up again, we pack up and go to one of the team's other fossil localities to dig for the rest of the afternoon.

Following what has already become the routine, we return to camp by six. Several people attend to the filtering of the drinking water while the rest help to prepare dinner. During the "cocktail hour" of warm beer and a shared plate of peanuts, Flynn and Wyss log the day's events and catalogue any interesting specimens they have collected. Others write field notes and letters home by the light of their headlamps. By nine, bellies full and dishes washed, people have retired to their tents. Camp is silent, the end of another day's efforts to uncover the past. —*K.W.*

Kate Wong *is a senior editor at* Scientific American.

PAY DIRT

ONE OF THE JOYS of working in little-charted terrain has been that if we manage to find anything, its scientific significance is virtually assured. That is why our first discoveries near Isalo National Park were so exciting. The same evening in 1996 that we found the rhynchosaur jaw fragments, then University of Antananarivo student Léon Razafimanantsoa spotted the six-inch-long skull of another interesting creature. We immediately identified the animal as a peculiar plant eater, neither mammal nor reptile, called a traversodontid cynodont [*see illustration on page 35*].

The rhynchosaur jaws and the exquisite traversodontid skull—the first significant discoveries of our ongoing U.S.-Malagasy project—invigorated our expedition. The first fossil is always the hardest one to find; now we could do the detailed collecting necessary to

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INSPECTING THE ROCKS up close, author Flynn (*right*) and William F. Simpson work to ensure that no scraps of bone have been overlooked.

NEITHER REPTILE NOR MAMMAL, this leopard-sized traversodontid, named *Menadon*, had the stout incisors and wide cheek teeth needed to grasp and grind vegetation as it browsed in Madagascar about 230 million years ago.

begin piecing together an image of the past. The white sandstones we were excavating had formed from the sand carried by the rivers that poured into lowlands as Madagascar unhinged from Africa. Within these prehistoric valleys rhynchosaurs and traversodontids, both four-legged creatures ranging from three to 10 feet in length, probably grazed together much the same way zebras and wildebeests do in Africa today. The presence of rhynchosaurs, which are relatively common in coeval rocks around the world, narrowed the date to sometime within the Triassic period (the first of three Mesozoic time intervals), which spans from 252 million to 201 million years ago. And because traversodontids were much more diverse and abundant during the first half of the Triassic than during the second, we thought initially that this scene played out before about 230 million years ago.

During our second expedition, in 1997, a third type of animal challenged our sense of where we were in time. Shortly after we arrived in southwestern Madagascar, one of our field assistants, a local resident named Mena, showed us some bones that he had found across the river from our previous localities. We were struck by the fine-grained red rock adhering to the bones—everything we had found until that point was buried in the coarse white sandstone. Mena led us about half a mile north of the rhynchosaur and traversodontid site to the bottom of a deep gully. Within a few minutes we spotted the bone-producing layer from which his unusual specimens had rolled. A rich concentration of fossils was entombed within the three-foot-thick layer of red mudstones, which had formed in the floodplains of the same ancient rivers that deposited the white sands. Excavation yielded about two dozen specimens of what seemed at first to be dinosaurs. Our team found jaws, strings of vertebrae, hips, claws, an articulated forearm with some wrist bones, and other assorted skeletal elements. When we examined the jawbones more closely, we realized that we had uncovered remains of a new species that resembled an enigmatic animal from Morocco called *Azendohsaurus*, at the time considered a prosauropod dinosaur. (Prosauropods, which typically appear in rocks between 225 million and 190 million years old, are smaller-bodied precursors of the long-necked sauropod dinosaurs.)

Much to our surprise, however, as the other bones were later cleaned from the rock and as we found additional bones over subsequent field seasons, we realized we were dealing with a perplexing early lineage of reptiles rather than a true dinosaur. This mysterious animal has teeth and some skull features that look just like those of typical prosauropods, but the rest of its skeleton is strikingly more primitive than any known dinosaur. We have not yet completely analyzed the unexpected combination of bones and teeth, but this evolutionary chimera—mixing characteristics of distantly related reptile groups—has led us to question whether certain features long believed to characterize dinosaurs might have evolved much earlier. If so, the new Malagasy fossil, *Azendohsaurus madagaskarensis*, and other animals long assumed to be dinosaurs are likely something else entirely.

WE HAD UNEARTHED A COLLECTION OF FOSSILS NOT KNOWN TO COEXIST ANYWHERE ELSE.

When we discovered that *Azendohsaurus* was foraging alongside rhynchosaurs and traversodontids, it became clear that we had unearthed a collection of fossils not known to coexist anywhere else. In Africa, South America and other parts of the world, traversodontids are much less abundant and less diverse once dinosaurs appear. Similarly, the most common type of rhynchosaur we found, *Isalorhynchus,* lacks advanced characteristics and thus is inferred to be more ancient. What is more, the Malagasy fossil assemblage lacks remains of several younger reptile groups usually found with the earliest dinosaurs, including the heavily armored, crocodilelike phytosaurs and aetosaurs. The mixture of ancient kinds of animals found alongside our enigmatic reptile, plus the lack of younger creatures, suggests that the Malagasy fossil deposit is as old as any dinosaur ever discovered, if not older.

Just one early dinosaur site—at Ischigualasto, Argentina—contains a rock layer that has been dated directly; all other early dinosaur sites with similar fossils are thus estimated to be no older than its radioisotopic age of about 228 million years. (Reliable radioisotopic ages are obtainable only from rock layers produced by contemporaneous volcanoes. The Malagasy sediments accumulated with no volcanoes nearby.) Based on the fossils present, we have tentatively concluded that our fossil-bearing rocks slightly predate the Ischigualasto time span. And because different major branches of the dinosaur evolutionary tree are already present at

MARIA STENZEL *National Geographic Image Collection* (*left*); JOHN WEINSTEIN *The Field Museum (Image ID GE086110_1c)* (*right*)

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Living in Mixed Company

Paleontologists did not know until recently that the unusual group of ancient animals shown above—*Azendohsaurus* (*1*), traversodontids (*2*), rhynchosaurs (*3*) and chiniquodontids (*4*)—once foraged together. In the past 18 years, southwestern Madagascar has become the first place where bones of each particular type of animal have been unearthed alongside the others, in this case from Triassic rocks about 230 million years old. Then the region was a lush, lowland basin that was forming as the supercontinent Pangaea began to break up. The long-necked *Azendohsaurus* pair here, which may have lived alongside the earliest dinosaurs, browse on conifers while a parrot-beaked rhynchosaur prepares to sip from a nearby pool. The prosauropodlike teeth of *Azendohsaurus* were spear-shaped and serrated—good for slicing vegetation; rhynchosaurs were perhaps the most common group of plant eaters in the area at that time. Foraging among these large reptiles are the peculiar traversodontids and chiniquodontids—early members of the Cynodontia, a broad group that includes today's mammals. The grinding cheek teeth of the traversodontids suggest that they were herbivores; the chiniquodontids sport the sharp, pointed teeth of carnivores. *—J.J.F. and A.R.W.*

Illustration by Frank Ippolito

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FINDINGS

Modern-Day Mystery

Madagascar is famous for its roughly 80 species of lemurs, none of which occurs anywhere else in the world. The same is true for 80 percent of the island's plants and other animals. This biotic peculiarity reflects the island's lengthy geographical isolation. Madagascar has not been connected to another major landmass since it separated from India nearly 90 million years ago, and it has not been joined with its nearest modern neighbor, Africa, since about 160 million years ago. But scant fossil evidence meant that little was known about the origin of these unique creatures.

While our research group was probing Madagascar's Triassic- and Jurassic-age rocks, teams led by David W. Krause of Stony Brook University were unearthing a wealth of younger fossils in the island's northwestern region. These specimens, which date back some 70 million years, include more than three dozen species, none of which is closely related to the island's modern animals. This evidence implies that most modern vertebrate groups must have immigrated to Madagascar after this point.

The best candidate for a Malagasy motherland is Africa, and yet the modern faunas of the two landmasses are markedly distinct. Elephants, cats, antelope, zebras, monkeys and many other modern African mammals apparently never reached Madagascar. The four kinds of terrestrial mammals that inhabit the island today—rodents, lemurs, carnivores and the hedgehoglike tenrecs—all appear to be descendants of more ancient African beasts. The route these immigrants took from the mainland remains unclear, however. Small clinging animals could have floated from Africa across the Mozambique Channel on "rafts" of vegetation that broke free during severe storms. Alternatively, when sea level was lower these pioneers might have traveled by land and sea along a chain of currently submerged highlands northwest of the island.

Together with Anne D. Yoder, now at Duke University, and others, we have used the DNA structure of modern Malagasy mammals to address this question. These analyses have revealed that the ancestor of Madagascar's modern carnivores arrived at a different time than the island's other mammal groups, each of which colonized the island in separate, long-distance dispersal events rather than a single episode. *—J.J.F. and A.R.W.*

Ischigualasto, the common ancestor of all dinosaurs must be older still. Rocks from before about 245 million years ago have been moderately well sampled around the world, but none of them has yielded dinosaurs. That means the search for the common ancestor of all dinosaurs must focus on a relatively poorly known and ever narrowing interval of Middle Triassic rocks, between about 240 million and 230 million years old.

MOSTLY MAMMALS

DINOSAURS NATURALLY ATTRACT considerable attention, being the most conspicuous land animals of the Mesozoic. Less widely appreciated is the fact that mammals and dinosaurs sprang onto the evolutionary stage at nearly the same time. At least two factors account for the popular misconception that mammals arose only after dinosaurs became extinct: Early mammals were all chipmunk-sized or smaller, so they don't grab the popular imagination. In addition, the fossil record of early mammals is sparse. To our delight, Madagascar has once again filled in two mysterious gaps in the fossil record. The traversodontid cynodonts from the Isalo deposits reveal new details about close mammalian relatives, and a younger fossil from the northwestern side of the island poses controversial questions about where and when a key advanced group of mammals got its start.

The Malagasy traversodontids, the first known from the island, include some of the best-preserved representatives of early cynodonts ever discovered. (Cynodontia is a broad group of land animals that includes mammals and their nearest relatives.) Accordingly, these bones provide a wealth of new anatomical information. These cynodonts are identified by, among other features, a simplified lower jaw dominated by a single bone, the dentary. Some specimens include both skulls and skeletons. Understanding the complete morphology of these animals is crucial for resolving the complex evolutionary transition from the large cold-blooded, scale-covered animals with sprawling limbs (which dominated the continents prior to the Mesozoic) to the much smaller warm-blooded, furry animals with an erect posture that are so plentiful today.

Many kinds of mammals, with many anatomical variations, now inhabit the planet. But they all share a common ancestor marked by a single, distinctive suite of features. To determine what these first mammals looked like, paleontologists must examine their closest evolutionary relatives within the Cynodontia, which include the traversodontids and their much rarer cousins, the chiniquodontids (also known as probainognathians), both of which we have found in southwestern Madagascar. Traversodontids almost certainly were herbivorous because their wide cheek teeth are designed for grinding—evidence of which we and our colleagues documented with scanning electron microscope analyses of microwear features on the teeth. The chiniquodontids, in contrast, were undoubtedly carnivorous, with sharp, pointed teeth. Most paleontologists agree that some chiniquodontids share a more recent common ancestor with mammals than the herbivorous traversodontids do. The chiniquodontid skulls and skeletons we found in Madagascar will help reconstruct the bridge between early cynodonts and true mammals.

Not only are Madagascar's Triassic cynodonts among the best preserved in the world, they also sample a time period that is poorly known elsewhere. The same is true for the youngest fossils our expeditions have uncovered—those from a region of the northwest where the sediments are about 165 million years in age. (That date falls within the middle of the Jurassic, the second of the Mesozoic's three periods.) Because these sediments were considerably younger than our Triassic rocks, we allowed ourselves the hope that we might find remains of an ancient mammal. Not a single mammal had been recorded from Jurassic rocks of a southern landmass at that point, but this did nothing to thwart our motivation.

Once again, persistence paid off. During our 1996 field season, we had visited the village of Ambondromahabo after hearing local reports of abundant large fossils of the sauropod dinosaur *Lappa-*

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rentosaurus. Sometimes where large animals are preserved, the remains of smaller animals can also be found—though not as easily. We crawled over the landscape, eyes held a few inches from the ground. This uncomfortable but time-tested strategy turned up a few small theropod dinosaur teeth, fish scales and other bone fragments, which had accumulated at the surface of a small mound of sediment near the village. These unprepossessing fossils hinted that more significant items might be buried in the sediment below. We bagged about 200 pounds of sediment and washed it through mosquito-net hats back in the capital, Antananarivo.

During the subsequent years back in the U.S., while our studies focused on the exceptional Triassic material, the tedious process of sorting the Jurassic sediment took place. A dedicated team—Dennis Kinzig, Ross Chisholm and Warren Valsa, all then volunteers at the Field Museum in Chicago—spent many a weekend sifting through the concentrated sediment under a microscope in search of valuable flecks of bone or teeth. We did not think much about that sediment again until 1998, when Kinzig relayed the news that they had uncovered the partial jawbone of a tiny mammal with three grinding teeth still in place. We were startled not only by the jaw's existence but also by its remarkably advanced cheek teeth. The shapes of the teeth document the earliest occurrence of Tribosphenida, a group encompassing the vast majority of living mammals. We named the new species *Ambondro mahabo,* after its place of origin.

The discovery pushes back the range of this group of mammals by more than 25 million years and offers the first glimpse of mammalian evolution on the southern continents during the latter half of the Jurassic period. It shows that this subgroup of mammals may have evolved in the Southern Hemisphere rather than the Northern, as is commonly supposed. The information does not resolve the debate, but it does point out the precarious nature of long-standing assumptions rooted in a fossil record historically biased toward the Northern Hemisphere [*see box on page 32*].

PLANNING PERSISTENTLY

ALTHOUGH OUR TEAM has recovered a broad spectrum of fossils in Madagascar, scientists are only beginning to describe the Mesozoic history of the southern continents. The number of species of Mesozoic land vertebrates known from Australia, Antarctica, Africa and South America is probably on an order of magnitude smaller than the number of contemporaneous findings from the Northern Hemisphere. Clearly, Madagascar now ranks as one of the world's top prospects for paleontologists.

Often the most significant hypotheses about ancient life on earth can be suggested only after these kinds of new fossil discoveries are made. Our team's explorations provide two cases in point: some fossils long mistaken for early dinosaurs actually belong to a distantly related lineage of reptiles, and the existence of the tiny mammal at our Jurassic site implies that tribosphenic mammals may have originated in the Southern, rather than Northern, Hemisphere. The best way to bolster these proposals (or to prove them wrong) is to go out and uncover more bones. That is why the primary goal of our August-September 2003 expedition was the same as it had been for our previous five expeditions: find as many fossils as possible.

Our agenda typically includes digging deeper into known sites and surveying new regions, blending risky efforts with sure bets. No matter how carefully formulated, however, our plans are always subject to last-minute changes. In 2003 our most daunting challenge was the appearance of frenzied boomtowns.

INTO THE SUNSET: Authors Flynn (*right*) and Wyss ride back to camp after a long day's digging in southwestern Madagascar.

During our first three expeditions, we never gave a second thought to the gravels that overlay the Triassic rock outcrops in the southwestern part of the island. Little did we know that those gravels contain sapphires. By 1999 tens of thousands of people were scouring the landscape in search of these gems. The next year all our Triassic sites fell within sapphire-mining claims. Paleontologists are now required to get permission for entry from both the claim holder and the government. In addition to that extra set of hurdles, the miners' presence has created security problems.

Even without such logistical obstacles, it would require uncountable lifetimes to carefully survey all the island's untouched rock exposures. But now that we have seen a few of Madagascar's treasures, we are inspired to keep digging. SA

John J. Flynn and **André R. Wyss** have collaborated for more than 25 years on expeditions to the Rocky Mountains, Baja California, the Andes of Chile, and Madagascar. They also study the evolution of carnivores, including dogs, cats and seals. Flynn is Frick Curator of Fossil Mammals at the American Museum of Natural History in New York City and dean of that institution's Richard Gilder Graduate School. Wyss is professor of earth science at the University of California, Santa Barbara, and a research associate at the American Museum of Natural History. The authors thank the University of Antananarivo for its long-term collaboration and the National Geographic Society, the John C. Meeker family and the World Wildlife Fund for their exceptional support.

MORE TO EXPLORE

Natural Change and Human Impact in Madagascar. Edited by Steven M. Goodman and Bruce D. Patterson. Smithsonian Institution Press, 1997.

A Middle Jurassic Mammal from Madagascar. John J. Flynn, J. Michael Parrish, Berthe Rakotosaminimanana, William F. Simpson and André R. Wyss in *Nature,* Vol. 401, pages 57–60; September 2, 1999.

A Triassic Fauna from Madagascar, Including Early Dinosaurs. John J. Flynn, J. Michael Parrish, Berthe Rakotosaminimanana, William F. Simpson, Robin L. Whatley and André R. Wyss in *Science,* Vol. 286, pages 763–765; October 22, 1999.

The Natural History of Madagascar. Edited by Steven M. Goodman and Jonathan P. Benstead. University of Chicago Press, 2003.

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MARIA STENZEL *National Geographic Image Collection*

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TYRANNOSAURUS REX defends its meal, a *Triceratops*, from other hungry *T. rex*. Deinonychosaurs, the small creatures at the bottom left and right, wait for scraps left by the tyrant kings while pterosaurs circle overhead on this typical day almost 66 million years ago. Trees and flowering plants complete the landscape.

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BREATHING LIFE INTO *T. REX*

By analyzing previously overlooked fossils and by taking a second look at some old finds, paleontologists are providing the first glimpses of the actual behavior of the tyrannosaurs

By Gregory M. Erickson

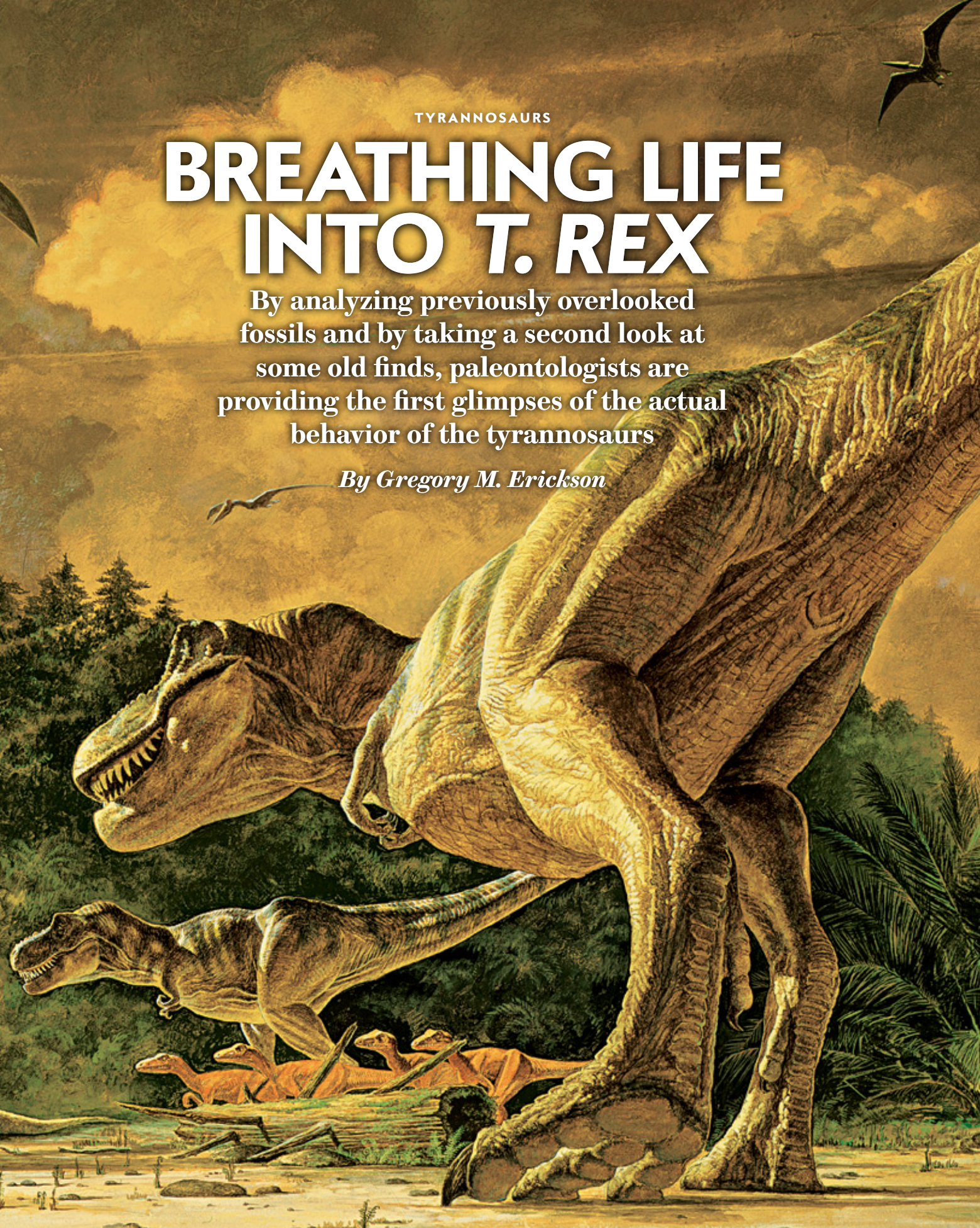

Illustration by Kazuhiko Sano

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DINOSAURS CEASED TO WALK THE EARTH 66 MILLION YEARS ago, yet they still live among us. Velociraptors star in movies, and *Triceratops* toys clutter toddlers' bedrooms. Of these charismatic animals, however, one species has always ruled our fantasies. Children, filmmaker Steven Spielberg and professional paleontologists agree that the superstar was and is *Tyrannosaurus rex*.

Harvard University paleontologist Stephen Jay Gould said that every species designation represents a theory about that animal. The very name *Tyrannosaurus rex*—"tyrant lizard king"—evokes a powerful image of this species. John R. Horner of Montana State University and science writer Don Lessem wrote in their book *The Complete* T. rex, "We're lucky to have the opportunity to know *T. rex,* study it, imagine it, and let it scare us. Most of all, we're lucky *T. rex* is dead." And paleontologist Robert T. Bakker, now at the Houston Museum of Natural Science, described *T. rex* as a "10,000-pound roadrunner from hell," a tribute to its obvious size and power.

In Spielberg's *Jurassic Park,* which at the time boasted the most accurate popular depiction of dinosaurs ever, *T. rex* was, as usual, presented as a killing machine whose sole purpose was aggressive, bloodthirsty attacks on helpless prey. *T. rex*'s popular persona, however, is as much a function of artistic license as of concrete scientific evidence. A century of study and the existence of 50 fairly complete *T. rex* specimens have generated substantial information about its anatomy and genealogical relationships. But inferring behavior from anatomy alone is perilous, and the true nature of *T. rex* continues to be largely shrouded in mystery. Whether it was even primarily a predator or a scavenger is still the subject of debate.

Over the past two decades, a new breed of scientist has begun to unravel some of *T. rex*'s better-kept secrets. These paleobiologists try to put a creature's remains in a living context—they attempt to animate the silent and still skeleton of the museum display. *T. rex* is thus changing before our eyes as paleobiologists use fossil clues, some new and some previously overlooked, to develop fresh ideas about the nature of these magnificent animals.

Rather than drawing conclusions about behavior based solely on anatomy, paleobiologists demand proof of actual activities. Skeletal assemblages of multiple individuals shine a light on the interactions among *T. rex* and between them and other species. In addition, so-called trace fossils reveal activities through physical evidence, such as bite marks on bones and wear patterns on teeth. Also of great value as trace fossils are coprolites, fossilized feces. (Remains of a herbivore, such as *Triceratops* or *Edmontosaurus,* in *T. rex* coprolites certainly provide smoking-gun proof of species interactions!)

One assumption that paleobiologists are willing to make is that closely related species may have behaved in similar ways. *T. rex* data are therefore being corroborated by comparisons with those of earlier members of the family Tyrannosauridae, including their geologically older cousins *Albertosaurus, Gorgosaurus* and *Daspletosaurus,* collectively known as albertosaurs.

SOLO OR SOCIAL?

TYRANNOSAURS are usually depicted as solitary, as was the case in *Jurassic Park*. (An alternative excuse for that film's loner is that the movie's genetic wizards wisely created only one.) Mounting evidence, however, points to gregarious *T. rex* behavior, at least for part of the animals' lives. Two *T. rex* excavations in the Hell Creek For-

IN BRIEF

Popular culture depicts *Tyrannosaurus rex* as a killing machine, but scientists are not even sure whether *T. rex* was primarily a predator or a scavenger.

Fossils are providing clues, such as bite marks and tooth-wear patterns, about how *T. rex* actually lived and what it ate. These clues suggest that tyrannosaurs were gregarious but sometimes fought viciously with one another.

***T. rex* may have used** its powerful jaws to pulverize herbivorous dinosaurs such as *Triceratops,* but evidence is sparse because collectors typically search for intact fossils rather than for chewed-up fragments.

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mation of eastern Montana are most compelling.

In 1966 Los Angeles County Museum researchers attempting to exhume a Hell Creek adult were elated to find another, smaller individual resting atop the *T. rex* they had originally sought. This second fossil was identified at first as a more petite species of tyrannosaur. My examination of the histological evidence—the microstructure of the bones—now suggests that the second animal was actually a subadult *T. rex* [*see top two micrographs on page 44*]. A similar discovery was made during the excavation of "Sue," one of the largest and most complete fossil *T. rex* ever found. Sue is perhaps as famous for its $8.36-million auction price following ownership haggling as for its paleontological status. Remains of a subadult and a juvenile *T. rex* were later found in Sue's quarry by researchers from the Black Hills Institute of Geological Research in Hill City, S.D. Experts who have worked the Hell Creek Formation, myself included, generally agree that long odds argue against multiple, loner *T. rex* finding their way to the same burial. The more parsimonious explanation is that the animals were part of a group.

An even more spectacular find from 1910 further suggests gregarious behavior among the Tyrannosauridae. Researchers from the American Museum of Natural History in New York City working in Alberta, Canada, found a bone bed—a deposit with fossils of many individuals—eventually found to hold at least 26 of *T. rex*'s close relatives, albertosaurs.

Philip J. Currie, now at the University of Alberta, and his team relocated the 1910 find and conducted the first detailed study of the assemblage. Such aggregations of carnivorous animals can occur when one after another gets caught in a trap, such as a mud hole or soft sediment at a river's edge, in which a prey animal that has attracted them is already ensnared. Under those circumstances, however, the collection of fossils should also contain those of the hunted herbivore. The general lack of such herbivore remains among the albertosaurs (and among the three–*T. rex* assemblage that included Sue) raises the possibility that this was a group that perished together from drought, disease or drowning.

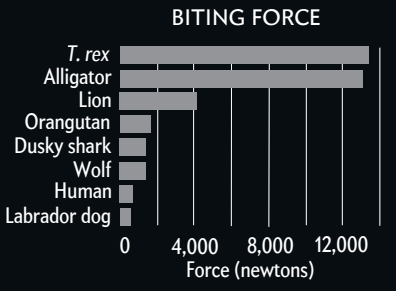
From examination of the remains collected so far, Currie estimates that the animals ranged from four to almost nine meters (13 to 29 feet) in length. This variation in size hints at a group composed of juveniles and adults that, based on my studies of growth lines in the bones, ranged in age from two to 28 years. Recent analysis of tracks shows evidence of tyrannosaurs moving together in pairs.

Tyrannosaurs in herds, with complex interrelationships, are in many ways an entirely new species to contemplate. But science has not morphed them into a benign and tender collection of Cretaceous Care Bears: some of the very testimony for *T. rex* group interaction is partially healed bite marks that reveal nasty interpersonal skills.

A paper published by Currie and Darren Tanke, both then at the Royal Tyrrell Museum in Alberta, highlights this evidence. Tanke is a leading authority on paleopathology—the study of ancient injuries and disease. He has detected a unique pattern of bite marks among theropods, the group of carnivorous dinosaurs that encompasses *T. rex* and other tyrannosaurs. These bite marks consist of gouges and punctures on the sides of the snout, on the sides and bottom of the jaws, and occasionally on the top and back of the skull.

Interpreting these wounds, Currie and Tanke reconstructed how these dinosaurs fought. They believe that the animals faced off but primarily gnawed at one another with one side of their complement of massive teeth rather than snapping from the front. The workers also surmise that the jaw-gripping behavior accounts for peculiar bite marks found on the sides of tyrannosaur teeth. The bite patterns imply that the combatants maintained their heads at the same level throughout a confrontation. Based on the magnitude of some of the fossil wounds, *T. rex* clearly showed little reserve in battle and sometimes inflicted severe damage on foes of its own species. One tyrannosaur studied by Tanke and Currie sports a souvenir tooth embedded in its own jaw, perhaps left by a fellow combatant.

The usual subjects—food, mates and territory—may have prompted the vigorous clashes among tyrannosaurs. Whatever the motivation behind the fighting, the fossil record demonstrates that the behavior was repeated throughout a tyrannosaur's life. Injuries among younger individuals seem to have been more common, possibly because a juvenile was subject to attack by members of its own age group as well as by large adults.



BITE-FORCE graph shows that *T. rex* is the undisputed champion. The author, working with bioengineer Dennis R. Carter and his students at Stanford University, simulated the production of feeding bite marks, which are typically less than full force, using a cast of a *T. rex* tooth on cow pelvises. They made a conservative estimate of approximately 13,300 newtons (about 3,000 pounds) for one side of the mouth. Most likely the contralateral teeth were also engaged, doubling the actual applied force.

BITES AND BITS

IMAGINE THE LARGE CANINE TEETH of a baboon or lion. Now imagine a mouthful of much larger canine-type teeth, the size of railroad spikes and with serrated edges. Kevin Padian of the University of California, Berkeley, has summed up the appearance of the huge daggers that were *T. rex* teeth: "lethal bananas."

Despite the obvious potential of such weapons, the general opinion among paleontologists had been that dinosaur bite marks were rare. The few published reports before 1990 consisted of brief com-

FRANÇOIS GOHIER *Photo Researchers, Inc* (*skull*); SARAH DONELSON (*graph*)

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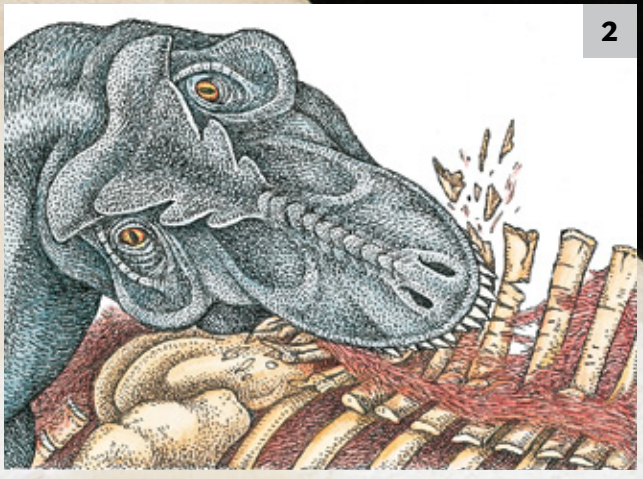

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1 NIPPING STRATEGY enabled *T. rex* to remove strips of flesh in tight spots, such as between vertebrae, using only the front teeth.
2 MASSIVE FORCE generated by *T. rex* in the "puncture and pull" biting technique was sufficient to have created indentations and furrows on the surfaces of the fossil bones of other dinosaurs. The enormous body of the *T. rex* (*skeleton above*) and its powerful neck musculature enabled the "pull" in "puncture and pull."

PATRICIA J. WYNNE (*illustrations on opposite page*); LOUIS PSIHOYOS *Matrix* (*photograph*)

ments buried in articles describing more sweeping new finds, and the clues in the marred remains concerning behavior escaped contemplation.

Some researchers have nonetheless speculated about the teeth. As early as 1973, Ralph E. Molnar, now at the Museum of Northern Arizona in Flagstaff, began musing about the strength of the teeth, based on their shape. Later, James O. Farlow of Indiana University–Purdue University Fort Wayne and Daniel L. Brinkman of Yale University performed elaborate morphological studies of tyrannosaur dentition, which made them confident that the "lethal bananas" were robust, thanks to their rounded cross-sectional configuration, and would endure bone-shattering impacts during feeding.

In 1992 I was able to provide material support for such speculation. Kenneth H. Olson, a Lutheran pastor and superb amateur fossil collector for the Museum of the Rockies in Bozeman, Mont., came to me with several specimens. One was a one-meter-wide, 1.5-meter-long partial pelvis from an adult *Triceratops*. The other was a toe bone from an adult *Edmontosaurus* (duck-billed dinosaur). I examined Olson's specimens and found that both bones were riddled with gouges and punctures up to 12 centimeters long and several centimeters deep. The *Triceratops* pelvis had nearly 80 such indentations. I documented the size and shape of the marks and used orthodontic dental putty to make casts of some of the deeper holes. The teeth that had made the holes were spaced some 10 centimeters apart. They left punctures with eye-shaped cross sections. They clearly included carinae, elevated cutting edges, on their anterior and posterior faces. And those edges were serrated. The totality of the evidence pointed to these indentations being the first definitive bite marks from a *T. rex*.

This finding had considerable behavioral implications. It confirmed for the first time the assumption that *T. rex* fed on its two most common contemporaries, *Triceratops* and *Edmontosaurus*. Furthermore, the bite patterns opened a window into *T. rex*'s actual feeding techniques, which apparently involved two distinct biting behaviors. *T. rex* usually used the "puncture and pull" strategy, in which biting deeply with enormous force was followed by drawing the teeth through the penetrated flesh and bone, which typically produced long gashes. In this way, a *T. rex* appears to have detached the pelvis found by Olson from the rest of the *Triceratops* torso. *T. rex* also employed a nipping approach in which the front (incisiform) teeth grasped and stripped the flesh in tight spots between vertebrae, where only the muzzle of the beast could fit. This method left vertically aligned, parallel furrows in the bone.

Many of the bites on the *Triceratops* pelvis were spaced only a few centimeters apart, as if the *T. rex* had methodically worked its way across the hunk of meat as we would nibble an ear of corn. With each bite, *T. rex* appears also to have removed a small section of bone. We presumed that the missing bone had been consumed, confirmation for which shortly came, and from an unusual source.

In 1997 Karen Chin, now at the University of Colorado, received a peculiar, tapered mass that had been unearthed by a crew from the Royal Saskatchewan Museum. The object, which weighed 7.1 kilograms and measured 44 by 16 by 13 centimeters, proved to be a *T. rex* coprolite [*see bottom photograph on next page*]. The specimen, the first ever confirmed from a theropod and more than twice as large as any previously reported meat eater's coprolite, was chock-full of pulverized bone. Once again making use of histological methods, Chin and I determined that the shattered bone came from a young herbivorous dinosaur. *T. rex* did ingest parts of the bones of its food sources

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and, furthermore, partially digested these items with strong enzymes or stomach acids.

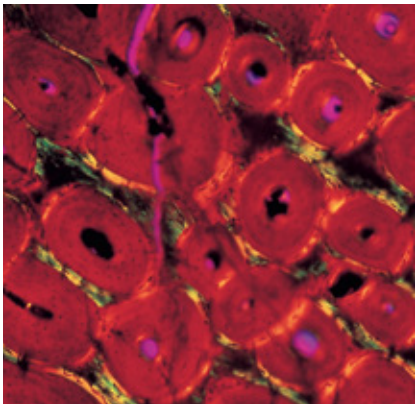
Following the lead of Farlow and Molnar, Olson and I have argued vehemently that *T. rex* probably left multitudinous bite marks, despite the paucity of known specimens. Absence of evidence is not evidence of absence, and we believe two factors account for this toothy gap in the fossil record. First, researchers have never systematically looked for bite marks. Even more important, collectors have had a natural bias against finds that might display bite marks. Historically, museums desire complete skeletons rather than single, isolated parts. But whole skeletons tend to be the remains of animals that died from causes other than predation and were rapidly buried before being dismembered by scavengers. The shredded bits of bodies eschewed by museums, such as the *Triceratops* pelvis, are precisely those specimens most likely to carry the evidence of feeding.

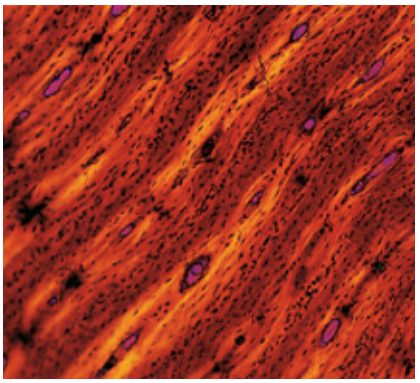
Indeed, Aase Roland Jacobsen of Århus University in Denmark surveyed isolated partial skeletal remains and compared them with nearly complete skeletons in Alberta. She found that 3.5 times as many of the individual bones (14 percent) bore theropod bite marks as did the less disrupted remains (4 percent). I view the majority of the world's natural history museums as deserts of behavioral evidence when compared with fossils still lying in the field waiting to be discovered and interpreted.

HAWK OR VULTURE?

SOME FEATURES of tyrannosaur biology, such as coloration, vocalizations or mating displays, may remain mysteries. But their feeding behavior is accessible through the fossil record. The collection of more trace fossils may finally settle a great debate in paleontology—the century-old controversy over whether *T. rex* was a predator or a scavenger.

When *T. rex* was first found a century ago, scientists immediately labeled it a predator. But sharp claws and powerful jaws do not necessarily a predator make. For example, most bears are omnivorous and kill only a small proportion of their food. In 1917 Canadian paleontologist Lawrence Lambe examined a partial albertosaur skull and inferred that tyrannosaurs fed on soft, rotting carrion. He came to this conclusion after noticing that the teeth were relatively free of wear. (Future research would show that 40 percent of shed tyrannosaur teeth are severely worn and broken, damage that occurs in a mere two to three years, based on my estimates of their rates of tooth replacement.) Lambe thus established the minority view that the beasts were in fact giant terrestrial "vultures." The ensuing arguments in the predator-scavenger dispute have centered on the anatomy and physical capabilities of *T. rex,* leading to a tiresome game of point/counterpoint.





BONE MICROSTRUCTURE reveals the maturity of the animal under study. Older individuals have bone consisting of Haversian canals (*large circles, top*), bone tubules that have replaced naturally occurring microfractures in the more randomly oriented bone of juveniles (*bottom*). Microscopic examination of bone has shown that individuals thought to be members of smaller species are in fact juvenile *T. rex*.

KING-SIZE COPROLITE, 44 centimeters long, is the largest of its kind from a carnivorous animal, more than twice the size of any previously reported. Its size, age, contents and geographical context rule out anything other than a tyrannosaur, and most likely a *T. rex*, as its producer.

Scavenger advocates adopted the "weak tooth theory," which maintained that *T. rex*'s elongate teeth would have failed in predatory struggles or in bone impacts. They also contended that its diminutive arms precluded lethal attacks and that *T. rex* would have been too slow to run down prey.

Predator supporters answered with biomechanical data. They cited my own bite-force studies that demonstrate that *T. rex* teeth were actually quite robust. (I personally remain uncommitted in this argument, pending the discovery of a greater body of evidence.) They also noted that Kenneth Carpenter of Utah State University Eastern and Matthew Smith, then at the Museum of the Rockies, estimated that the "puny" arms of a *T. rex* could curl nearly 180 kilograms. And they pointed to the work of Per Christiansen of the University of Copenhagen, who believes, based on limb proportions, that *T. rex* may have been able to sprint at 47 kilometers an hour (29 miles an hour). Subsequent studies suggest that a speed of 24 to 37 kilometers per hour is more likely and that adults ambled rather than ran. Regardless of which estimate is correct, such speed would be faster than that of any of *T. rex*'s large herbivorous contemporaries. (Speed is not the only factor in predation, of course. Acceleration, stealth, endurance, agility, experience and guile—all of which are difficult to quantify—are also important considerations, as are size differences and prey availability and vulnerability.)

Even biomechanical studies fail to resolve the predator-scavenger debate—and they never will. The critical determinant of *T. rex*'s ecological niche is discovering how and to what degree it utilized the animals living and dying in its environment, rather than establishing its presumed adeptness for killing. Both sides concede that predatory animals, such as lions, will scavenge and that classic scavengers, such as vultures, will sometimes kill. And mounting physical evidence leads to the conclusion that tyrannosaurs both hunted and scavenged.

Within *T. rex*'s former range exist bone beds consisting of hundreds and sometimes

GREGORY M. ERICKSON (*top*); COURTESY OF ROYAL SASKATCHEWAN MUSEUM (*bottom*)

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thousands of edmontosaurs that died from floods, droughts and causes other than predation. Bite marks and shed tooth crowns in these edmontosaur assemblages attest to scavenging behavior by *T. rex*. Jacobsen has found comparable evidence for albertosaur scavenging. Robert A. DePalma of the Palm Beach Museum of Natural History in Florida, David A. Burnham of the University of Kansas and their colleagues, on the other hand, have provided solid evidence of predatory behavior in the form of an unsuccessful attack by a *T. rex* on an adult hadrosaur, likely an *Edmontosaurus*. The intended prey purportedly escaped with damaged tailbones that later healed. The culprit left its calling card—an embedded broken tooth! Similar evidence has been found in other edmontosaurs and possibly in *Triceratops*.

Quantification of such discoveries could help determine the degree to which *T. rex* undertook each method of obtaining food, and paleontologists could avoid future arguments by adopting standard definitions of predator and scavenger. Such a convention is necessary because a wide range of views pervades vertebrate paleontology as to what exactly makes for each kind of feeder. For example, some extremists contend that if a carnivorous animal consumes any carrion at all, it should be called a scavenger. But such a constrained definition negates a meaningful ecological distinction because it would include nearly all the world's carnivorous birds and mammals.

TRACE FOSSILS MAY SETTLE A CENTURY-OLD DEBATE: WAS *T. REX* A PREDATOR OR SCAVENGER?

In a definition more consistent with most paleontologists' commonsense categorization, a predatory species would be one in which most individuals acquire most of their meals from animals they or their peers killed. Most individuals in a scavenging species, on the other hand, would not be responsible for the deaths of most of their food.

Trace fossils could open the door to a systematic approach to the predator-scavenger controversy, and the resolution could come from testing hypotheses about entire patterns of tyrannosaur feeding preferences. For instance, Jacobsen has pointed out that evidence of a preference for less dangerous or easily caught animals supports a predator niche. Conversely, scavengers would be expected to consume all species equally.

Within this logical framework, Jacobsen has compelling data supporting predation. She surveyed thousands of dinosaur bones from Alberta and learned that unarmored hadrosaurs are twice as likely to bear tyrannosaur bite marks as are the more dangerous horned ceratopsians. Tanke, who participated in the collection of these bones, relates that no bite marks have been found on the heavily armored, tanklike ankylosaurs.

Jacobsen cautions, though, that other factors confuse this set of findings. Most of the hadrosaur bones are from isolated individuals, but most ceratopsians in her study are from bone beds. Again, these beds contain more whole animals that have been fossilized unscathed, creating the kind of tooth-mark bias discussed earlier. A survey of isolated ceratopsians would be enlightening. And analysis of more bite marks that reveal failed predatory attempts, such as those reported by DePalma, Burnham and their colleagues, could also turn up preferences, or the lack thereof, for less dangerous prey.

Jacobsen's finding that cannibalism among tyrannosaurs was rare—only 2 percent of albertosaur bones had albertosaur bite marks, whereas 14 percent of herbivore bones did—might also support predatory preferences instead of a scavenging niche for *T. rex,* particularly if these animals were in fact gregarious. Assuming that they had no aversion to consuming flesh of their own kind, it would be expected that at least as many *T. rex* bones would exhibit signs of *T. rex* dining as do herbivore bones. A scavenging *T. rex* would have had to stumble on herbivore remains, but if *T. rex* traveled in herds, freshly dead conspecifics would have been easy to find.

Coprolites may also provide valuable evidence about whether *T. rex* had any finicky eating habits. Because histological examination of bone found in coprolites can give the approximate stage of life of the consumed animal, Chin and I have suggested that coprolites may reveal a *T. rex* preference for feeding on vulnerable members of herds, such as the very young. Such a bias would point to predation, whereas a more impartial feeding pattern, matching the normal patterns of attrition, would indicate scavenging. Meaningful questions may lead to meaningful answers.

In the past century, paleontologists have recovered enough physical remains of *Tyrannosaurus rex* to give the world an excellent idea of what these monsters looked like. The attempt to discover what *T. rex* actually *was* like relies on those fossils that carry precious clues about the daily activities of dinosaurs. Paleontologists now appreciate the need for reanalysis of finds that were formerly ignored and have recognized the biases in collection practices, which have clouded perceptions of dinosaurs. The intentional pursuit of behavioral data should accelerate discoveries of dinosaur paleobiology. And new technologies may tease information out of fossils that we currently deem of little value. The *T. rex,* still alive in the imagination, continues to evolve. SA

Gregory M. Erickson is a professor of biological science at Florida State University and has studied dinosaurs since his first expedition to Montana's Hell Creek Formation badlands in 1986. He received his undergraduate degree in geological sciences from the University of Washington, his master's in biology from Montana State University and a doctorate in integrative biology from the University of California, Berkeley. Before coming to Florida State, he conducted postdoctoral research in bioengineering at Stanford University and in ecology and evolution at Brown University. Tyrannosaurs are Erickson's favorite study animals. He has spent the past few summers excavating their remains on the North Slope of Alaska. He has won the Romer Prize from the Society of Vertebrate Paleontology, the Stoye Award from the American Society of Ichthyologists and Herpetologists, and the Davis Award from the Society for Integrative and Comparative Biology. In 2012 he was elected as a fellow of the American Association for the Advancement of Science.

MORE TO EXPLORE

The Complete *T. Rex*. John R. Horner and Don Lessem. Simon & Schuster, 1993.

Bite-Force Estimation for *Tyrannosaurus rex* from Tooth-Marked Bones. Gregory M. Erickson, Samuel D. Van Kirk, Jinntung Su, Marc E. Levenston, William E. Caler and Dennis R. Carter in *Nature,* Vol. 382, pages 706–708; August 22, 1996.

A King-Sized Theropod Coprolite. Karen Chin, Timothy T. Tokaryk, Gregory M. Erickson and Lewis C. Calk in *Nature,* Vol. 393, pages 680–682; June 18, 1998.

Gigantism and Comparative Life-History Parameters of Tyrannosaurid Dinosaurs. Gregory M. Erickson, Peter J. Makovicky, Philip J. Currie, Mark A. Norell, Scott A. Yerby and Christopher A. Brochu in *Nature,* Vol. 430, pages 772–775; August 12, 2004.

Tyrannosaur Life Tables: An Example of Nonavian Dinosaur Population Biology. Gregory M. Erickson, Philip J. Currie, Brian D. Inouye and Alice A. Winn in *Science,* Vol. 313, pages 213–217; June 14, 2006.

Tyrannosaur Paleobiology: New Research on Ancient Exemplar Organisms. Stephen L. Brusatte, Mark A. Norell, Thomas D. Carr, Gregory M. Erickson, John R. Hutchinson, Amy M. Balanoff, Gabe S. Bever, Jonah N. Choiniere, Peter J. Makovicky and Xing Xu in *Science,* Vol. 329, pages 1481–1485; September 17, 2010.

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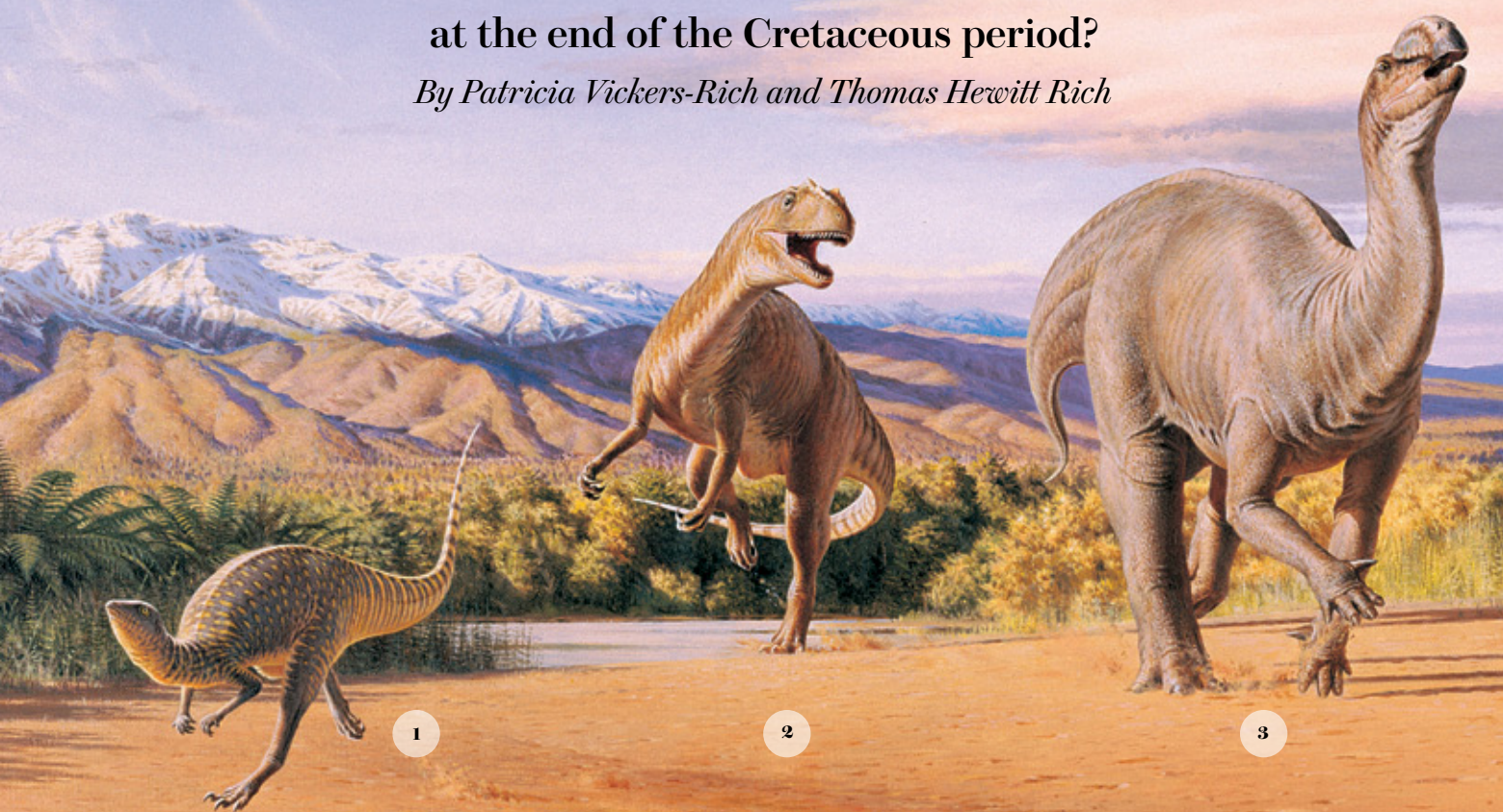
CLIMATE

DINOSAURS OF POLAR AUSTRALIA

Their excellent night vision and apparent warm blood raise a question: Could they have survived icehouse conditions at the end of the Cretaceous period?

By Patricia Vickers-Rich and Thomas Hewitt Rich



DINOSAURS flourished in southeastern Victoria during the Early Cretaceous, when the region lay within the Antarctic Circle. This mural depicts six species that left fossils there and a seventh—the large iguanodontid *Muttaburrasaurus*—that has been found only in Queensland, far to the north. The paucity of large polar dinosaurs may reflect a real absence or merely the selective preservation of small bones. Peter Trusler painted the mural of the creatures, which was created for an Australia Post stamp issue entitled "Australia's Dinosaur Era."

1. *LEAELLYNASAURA*
2. *AUSTRALOVENATOR*
3. *MUTTABURRASAURUS*
4. PTEROSAUR (FLYING)
5. ANKYLOSAUR
6. *ATLASCOPCOSAURUS*
7. ORNITHOMIMOSAUR

Illustrations by Peter Trusler

IN THE EARLY CRETACEOUS PERIOD, JUST OVER 100 MILLION YEARS AGO, AUSTRALIA LAY alongside Antarctica, which straddled the South Pole as it does today. Australia's southeastern corner, now the state of Victoria, lay well inside the Antarctic Circle. At that time, the region hosted an assemblage of animals and plants that lived under climate conditions having no modern analogue. The average temperature appears to have ranged from frigid to low temperate. Through the long winter, the sun did not shine for weeks or months at a time.

Many dinosaur lineages survived in this strange environment after they had died out in other places. At least one member of the group evolved an adaptation to the cold and to the dark that is interesting both in itself and for what it tells of the passing of a biological epoch. If global cooling indeed killed the dinosaurs, as many paleontologists have suggested, then Australia's species were the ones most likely to have survived the longest. Did their adaptations to an already marginal climate help them survive a sharp cooling trend, one that caught species living on other continents unprepared?

Although the Cretaceous fossil plants of southeastern Australia have been studied for more than a century, the animals remained mostly hidden until recently. In 1903 geologist William Hamilton Ferguson found two bones that have had a bearing on later paleontological work—the tooth of a lungfish and the claw of a carnivorous dinosaur, assigned to the theropod genus *Megalosaurus*. For the next 75 years, as no further finds joined them, these bones lay neglected in a cabinet in Museum Victoria. Then, in 1978, two graduate students at Monash University, Tim F. Flannery and John A. Long, discovered near Ferguson's original site the first specimens of a trove of dinosaur bones embedded in sediments from the Early Cretaceous.

These discoveries—only an hour and a half's drive southeast of Melbourne—encouraged paleontologists to prospect other coastal sites. In 1980 we struck a rich lode in the Otway ranges, which the Victorian government, at our suggestion, has since named Dinosaur Cove. There, for a decade—with the help of Earthwatch and other volunteers, the National Geographic Society, the Australian Research Council and Atlas Copco, a manufacturer of mining equipment—we spent three months out of every year chiseling, hammering and on occasion blasting tunnels into the fossil-bearing strata. With Dinosaur Cove worked out in 1994, effort has since been concentrated at a site about 200 kilometers east, called Flat Rocks. The rocks there are about 10 million years older than those at Dinosaur Cove.

Sediments at Flat Rocks, Dinosaur Cove and other sites of similar character were formed when violent, seasonal streams swept broad floodplains of their accumulated bones and plant life, depositing this flotsam and jetsam at the bottom of shallow stream channels. These deposits appear along the southern Victorian shore because only there could gnawing waves expose the sediments laid down in the rift valley that formed when Australia and Antarctica went their separate ways, as did the other fragments of Gondwana, an ancient supercontinent [*see box on opposite page*]. Only three fossil sites from the same period have been found inland, one in sediments laid down under far quieter conditions at the bottom of an ancient lake. This inland site has therefore yielded some uncommonly well preserved specimens. It must

IN BRIEF

More than 100 million years ago, Australia's southeastern corner, in what is now the state of Victoria, lay inside the Antarctic Circle.

At that time, polar Australia fell into total darkness for at least six straight weeks during winter, and the average annual temperature was only mildly temperate, if not freezing.

Polar Victoria was home to at least nine types of carnivorous theropod dinosaurs during the Cretaceous, as well as to horned dinosaurs that may have arisen in the southern continent.

The dinosaurs of polar Australia appear to have been, for the most part, relatively small, perhaps because they were trapped on a peninsula of the landmass and could not easily migrate.

"Hypsilophodontid" dinosaurs, which resemble wallabies in body shape and ecological role, are prominent in Victoria's fossil record. Their large eyes probably made it easier to forage during the long winter's night. Such adaptations may have enabled Victoria's dinosaurs to survive longer than dinosaurs in other parts of the world.

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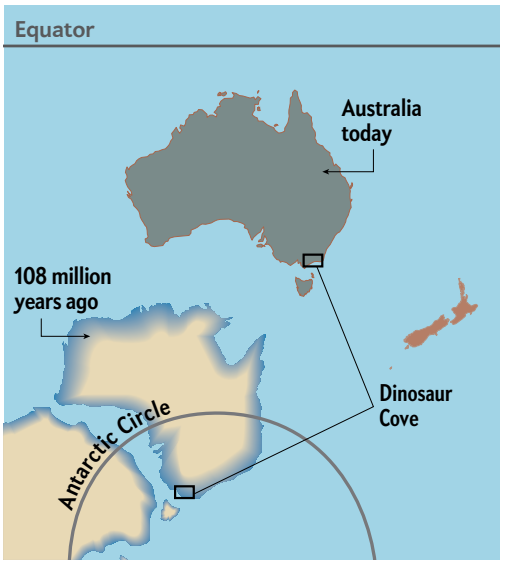
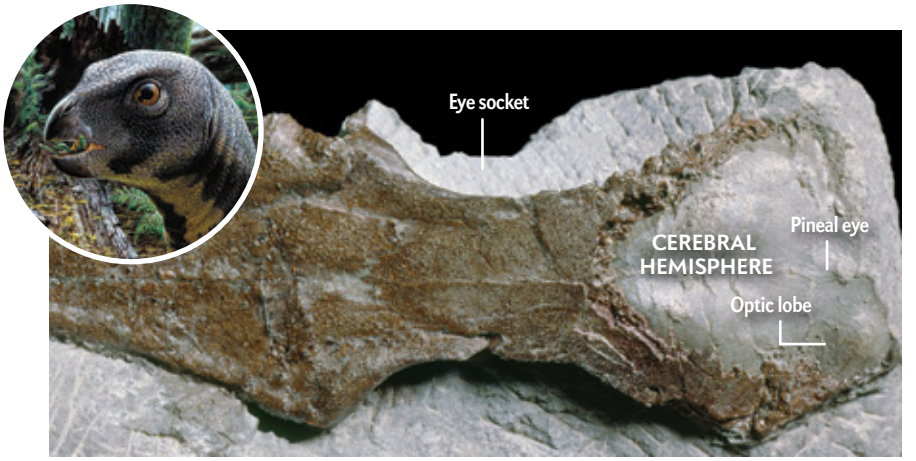
The Fossils of Dinosaur Cove



The southern supercontinent known as Gondwana began to break up more than 100 million years ago, when a rift valley formed between what would become Australia and Antarctica (*left*). Stream channels in the valley accumulated bones gathered by floodwaters that periodically swept these broad plains. The bones, together with clay and silt, produced the fossil-bearing formations of Dinosaur Cove (*right*).



Acute night vision is suggested by the brain structure and large eyes of *Leaellynasaura amicagraphica*. A huge optic lobe can be seen at the rear of this natural brain cast (*right, enlarged*). Large eyes were common to all hypsilophodontids, including *Qantassaurus intrepidus* (*inset*), a close relative of *L. amicagraphica,* and may have helped the group dominate an environment marked by seasonal darkness.

be noted that southeastern Australia's dinosaurs are known from about 8,000 individual bones and four partial skeletons. Only a few hundred of the bones can be assigned to a given species or genus. What they lack in number, however, they make up for in scientific interest.

All efforts at interpretation revolve around the estimation of temperature, for which three methods have been tried. Robert T. Gregory of Southern Methodist University and his associates infer Australian paleoclimate from the ratio of oxygen 18 to oxygen 16 trapped in concretions in ancient rocks. They find that mean annual temperatures probably approached zero degrees Celsius but might have reached as high as eight degrees C. Such values occur today in Hudson Bay, Saskatchewan (zero degrees C), and in Minneapolis and Toronto (eight degrees C).

Work by Andrew Constantine of Origin Energy on structures preserved in the rocks near where the dinosaur bones are buried provides evidence for the former existence of permafrost and ice wedging, as well as patterned ground and hummocky ground. Such features are formed today in regions with mean annual temperatures of three degrees C below zero to three degrees C above zero. These structures are most obvious only three meters stratigraphically below the Flat Rocks locality where dinosaurs and mammals have been found. Evidence for the occurrence of permafrost had never before been reported in association with dinosaurs.

Robert A. Spicer of the Open University in the U.K. and Judith Totman Parrish of the University of Idaho instead deduce temperature from the structure of ancient plants, arriving at the somewhat higher mean annual temperature of 10 degrees C. Their

JOHNNY JOHNSON (*top left*); PETER MENZEL; COURTESY OF NATIONAL GEOGRAPHIC SOCIETY (*top right*); PETER TRUSLER (*bottom inset illustration*); STEVE MORTON *Monash University (bottom photograph)*

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research with colleagues has demonstrated that polar Australia supported conifers, ginkgoes, ferns, cycads, bryophytes and horsetails but only a few angiosperms, or flowering plants, identifiable by a sprinkling of pollen. The angiosperms were then just beginning to spread into new niches. Perhaps they got their start by exploiting weedy ecological systems in the rift valleys that formed as the supercontinent split apart.

Spicer and Parrish noticed that evergreens, which provided forage in all seasons, had thick cuticles and other structural features that indicate adaptation to cold or dryness (perhaps brought on by winter freezing). Deciduous plants offer another climatic clue: they seem to have lost all their leaves at once. These mass falls may have been triggered by darkness or cold. Drought, however, probably did not serve as a constant cue—the sedimentary record and the abundance of ferns and bryophytes argue for conditions that were moist in all seasons except perhaps winter.

SURVIVING THE COLD

IF THE HIGHER ESTIMATE of mean temperature is correct, Australia was both temperate and subject to a period of continuous darkness every year—a combination with absolutely no modern counterpart. The winter night lasted between six weeks and four and a half months, depending on the true paleolatitude. Because the lower extreme of temperature would then have fallen well below the mean, most of the vertebrates preserved as fossils must have lived quite close to their thermal limits. Some, such as lungfish, cannot now breed in waters colder than 10 degrees C.

If, on the other hand, the lower estimate is correct, it becomes more than a typical scientific challenge to understand how this paleocommunity functioned at all. Before seriously attacking this problem, scientists will first have to demonstrate that it exists. To refine the temperature estimate, a multidisciplinary team is comparing floral, geochemical and other forms of evidence.

Nothing in this fauna is quite so peculiar to the region as the koala is today, for although the species and genera were local, they belonged to cosmopolitan families. Yet their adaptations are striking, as is the fact that some survived beyond the time of demise for their families elsewhere.

Among such anachronisms—or relicts—are the temnospondyl amphibians, possibly ancestors of modern amphibians. Most paleontologists had thought this group went extinct by some 160 million years ago, in the Jurassic. In the past few decades, however, Michael Cleeland and Lesley Kool of Monash University found three jaws from this group in Victorian sediments dating from the Early Cretaceous. Two of the jaws were unmistakable because their teeth had the labyrinthine infolding of the enamel that gives this group its common name: labyrinthodonts. At least one large species of temnospondyl lived in polar Australia about 120 million years ago, several million years after the group had died out elsewhere.

How did they survive? We suspect that the cool weather preserved the animals from competition with crocodiles, which were probably poorly adapted to the conditions prevailing in southeastern Australia until the onset of climate warming during the last five million years of the Early Cretaceous. The hypothesis rests on the fact that contemporary crocodilians now live in waters no colder than 10 degrees C, whereas some modern frogs and salamanders can be active in meltwater from snow.

At least nine different types of carnivorous theropod dinosaurs once lived in what is now Victoria. *Australovenator* is known from a partial skeleton, about 5.5 meters long, found in northeastern Australia about 2,000 kilometers north of Victoria. It is an allosauroid and thus a relative of the well-known *Allosaurus* from North America and Africa. An ankle bone from Victoria appears to belong to either this same genus or one closely related to it.

HARD ROCK made hard work for these volunteer paleontologists at Dinosaur Cove. Full-scale mining techniques (*above*) and rock saws (*opposite page*) are used to extract fossil-bearing slabs, which tend to fracture along the planes containing the largest treasures.

A spinosaur, a type of theropod dinosaur with tall spines that projected above its back, might have been even larger. A single fragment of a vertebra is the only evidence that this primarily fish-eating animal once existed anywhere in Australia.

Also present in Victoria were at least seven smaller-bodied theropods. The one best represented in the fossil record, by numerous isolated bones and teeth, is another species of allosauroid. In stark contrast, each of the other six smaller-bodied species is represented by only one or a few isolated bones. This meagerness of evidence for the former presence of so many taxa suggests that more of these smaller-bodied theropods will be found with further work in Victoria.

Among the smaller theropods was *Timimus hermani,* known from only two bones. It was a tyrannosauroid distantly related to *Tyrannosaurus rex* and had unusually long and slender femora, suggesting it may have been particularly fleet-footed.

This tyrannosauroid and two other, smaller theropods—the ostrichlike ornithomimosaur and a possible oviraptorosaur dubbed "the egg thief"—are otherwise not known from Gondwana but are found on the northern continents. Whereas tyrannosauroids in the Northern Hemisphere significantly predate their Australian counterparts, the ornithomimosaur and oviraptorosaur, if they are correctly identified, first appeared during the same geologic period in both hemispheres.

Fossils of the other three smaller-bodied Victorian theropods—an allosauroid, a sickle-clawed dromaeosaurid and a horned ceratosaur—have been found elsewhere in Gondwana and the Northern Hemisphere.

Besides the theropods, another dinosaur group that has been

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identified belongs to the neoceratopsians, or horned dinosaurs. Identification is tentative because it is based on just two ulnae (part of the lower arm), but the similarity of one of them to *Leptoceratops,* a browser the size of a sheep, is uncanny. Previously, all neoceratopsian records dated from the Late Cretaceous and, with the exception of a few bones from Argentina, came from the Northern Hemisphere. Reports indicate the existence of Early Cretaceous neoceratopsians in Utah and China. This dinosaur family may also have arisen in the southern supercontinent.

In addition to dinosaurs, the region provides evidence for mammals that appear to be among the earliest members of their groups. The minuscule *Bishops* resembles the living spineless hedgehog *Neotetracus.* This animal may have been a placental. If so, it is as old as the oldest placentals reported from the Northern Hemisphere and twice the age of the oldest marsupial yet found in Australia. This age is surprising because the domination of Australia by marsupials today is typically explained as the result of land-dwelling placentals reaching the continent long after the marsupials.

Another mammalian group, whose presence is no surprise, comprises the monotremes. An isolated limb bone of one of them has a structure suggestive of a more upright stance than either the echidna or the platypus. A second species is by far the smallest monotreme, weighing only 1 percent as much as any other living or fossil member of the group.

The Australian Early Cretaceous also reshaped forms that continued to flourish in other regions. By far the most successful such group consisted of the "hypsilophodontid" dinosaurs, an informal subdivision of the basal Ornithopoda. These animals, most of them hardly larger than a chicken, were bipeds built for speed, with large hind legs, small but well-developed hands, substantial tails and—for the most part—herbivorous habits. They thus resembled wallabies in both shape and ecological role.

The family Hypsilophodontidae was common throughout the world from the Middle Jurassic to Late Cretaceous times, but its prominence reaches an absolute and relative peak in the Victorian sediments. Not only do hypsilophodontids constitute most of the dinosaur remains, they are also represented by four to five genera, depending on the taxonomic criteria one uses, and five to six species. Other areas, some much more richly endowed with dinosaur species, never harbored more than three kinds of hypsilophodontids at a time. Something clearly favored the diversification of this group in polar Australia.

BIG-EYED FORAGERS

A PARTICULARLY INTRIGUING adaptation of at least one species of polar hypsilophodontid is suggested by the magnificently preserved brain cast of *Leaellynasaura amicagraphica* (named after our daughter, along with friends of the Museum Victoria and the National Geographic Society). The brain, unusually large for a dinosaur of this size, bears the marks of optic lobes, the relative size of which is easily the greatest ever documented in a hypsilophodontid.

How is one to interpret these enlarged lobes? We hypothesize that they enhanced the animals' ability to see in the dark, enabling them to forage effectively during the long winter months. There would have been no lack of food then, for those capable of seeing it: the herbivores could have lived off evergreens and deciduous leaf mats, and the carnivores could have hunted the herbivores.

This hypothesis also explains why this group came to dominate the polar environment in the first place. Hypsilophodontids everywhere in the world had large eyes and, presumably, acute vision. That trait could have given them their foothold in polar Australia.

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LAST OF ITS KIND: ***Koolasuchus cleelandi,*** **the last surviving temnospondyl amphibian, floats in an autumn setting about 120 million years ago in southeastern Australia.**

Once established in this "protected" environment, the hypsilophodontids could have competed with one another to produce the observed diversity of genera and species, perhaps all sharing hypertrophied optic lobes.

If the animals foraged at night, they must have been active at freezing or subfreezing temperatures. This feat goes far beyond the cold tolerance of any modern reptile, even the New Zealand tuatara, *Sphenodon punctatus,* which can remain active at five degrees C, provided it can sun itself. *Leaellynasaura* could have survived solely by maintaining a constant body temperature, eating frequently, as birds do in wintertime.

Pterosaurs—the flying reptiles—and the heavily armored ankylosaurs also appear in the Victorian fossil record, but the remains are so fragmented that they tell us little about the animals' lives. Much can be gleaned from one handful of teeth, however, for they come from plesiosaurs. These reptiles, not themselves dinosaurs, generally paddled the seas, but here two plesiosaur species quite different from one another inhabited freshwater in the ancient valley between Australia and Antarctica. They thus recall the Ganges River dolphin, one of the few cetaceans that live in freshwater.

One of the two species may have been a pliosaur—a type of plesiosaur with a short neck and elongated skull—whose body was four meters or more in length. The other was a typically long-necked, small-skulled plesiosaur. This obvious difference in body plan may explain how the two plesiosaur species managed to coexist in the same environment, being adapted to feeding on quite different prey.

The sauropods are one of the few major dinosaur groups that are absent. These giants, familiar from the example of *Apatosaurus,* lived at that time in Australia's lower latitudes. Not one, however, has been found farther south.

The apparent restriction of these large dinosaurs to lower latitudes in the Cretaceous of Australia may be real or merely an artifact of sampling. We worry about this question because the floodwaters that broke out of rain-swollen rivers would have collected small and medium-size bones but left large ones. The body of a sauropod would have stayed put rather than floating to a place where many specimens were concentrated in the small flood channels, which were no more than five to 10 meters in width and 20 to 30 centimeters in depth. This factor may explain the absence of the large bones of sauropods but not their tiny teeth. Thus, they did not seem to have reached polar Australia, although their vertebrae are known from polar New Zealand and the Antarctic Peninsula.

Yet we suspect there was an underlying tendency toward small body size in these polar environs. None of the hypsilophodontids, it must be remembered, stood taller than a human, and most were barely knee-high. The ornithomimosaur is equally unprepossessing, and the protoceratopsid and the ankylosaur are each no bigger than a sheep. A single fragment of a claw constitutes our sole

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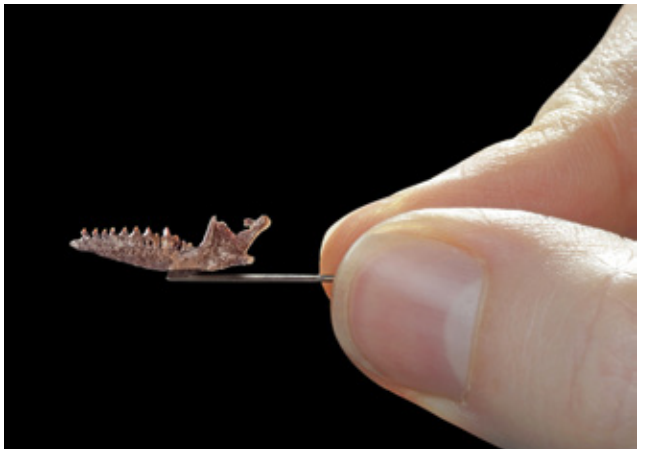

WHEN ALIVE during the Cretaceous, *Bishops* from southeastern Australia may have resembled the modern-day spineless hedgehog from China and Southeast Asia, *Neotetracus* (*top*). The jaw shows what is known of the fossil (*bottom*).

record of a large dinosaur—a carnivore, apparently similar to *Baryonyx* of England—which may have measured up to eight meters in length. The rare evidence for the largest dinosaur in polar Victoria is based on the smallest identifiable part of its skeleton. Thus, we cannot rule out the possibility that a systematic bias against the preservation of larger fossils is the reason that large dinosaurs rarely are found there. But although there is evidence for at least one large dinosaur in polar Victoria, the dinosaur assemblage does seem to have consisted primarily of smaller individuals.

This pattern contradicts the classic scaling laws formulated by Carl Bergmann and Joel Allen in the 19th century. According to these laws, animals in a given lineage tend to become larger and more compact as the average temperature of their environment falls. This trend is exemplified by the comparison of mountain lions in Canada with pumas of Central America and of human populations in the subarctic and tropical zones.

Other factors also determine body dimensions, especially the size of the territory in which a population lives. Individuals found on islands are often smaller than their mainland counterparts. For example, there were dwarf elephants on the ancient Mediterranean islands, and pygmy mammoths were found in 4,000-year-old sediments on islands off the north coast of Siberia. Dwarfism may be a response to selective pressure to increase the number of individuals so as to ensure a gene pool diverse enough for the species to survive in a restricted area. This effect has also been observed on peninsulas—and ancient southeastern Australia was a peninsula of the Gondwana landmass.

The dinosaurs on that peninsula were trapped virtually at the ends of the earth. Their direct path north was blocked by a vast inland sea, which they could have passed only by going hundreds of kilometers to the west before wheeling about to the north. At the end of such labors, they would have been able to catch, at most, an hour of sun a day in winter. Migration would have made little sense for such small animals.

Less formidable barriers sealed in the dinosaurs of the one other polar site that has yielded large quantities of fossils: the North Slope of Alaska. The dinosaurs there had a clear north-south corridor along which they could migrate with ease. It is significant that those dinosaurs were big—at least equal in size to caribou, wildebeest and other modern animals that migrate.

SAFE HAVEN IN GONDWANA

ONE MUST QUESTION whether animals so superbly adapted to the cold and the dark could have been driven to extinction by an artificial winter, such as is supposed to have followed a cataclysmic event at the boundary between the Cretaceous and Paleogene. It is proposed that the cataclysm, perhaps a combination of a collision with a comet or asteroid and a series of volcanic eruptions, suffused the atmosphere with a blanket of dust, excluding sunlight and freezing or starving most animals to death.

We suspect, however, that no such artificial winter could have killed the dinosaurs unless it lasted for a long time, certainly more than a few months. Otherwise at least a few of the polar dinosaurs would have survived the cataclysm. Of course, it is possible that a different development had already ended the reign of southern Australia's dinosaurs by the end of the Cretaceous.

English writer Arthur Conan Doyle once dreamed of a plateau in South America that time forgot, where dinosaurs continued to rule the land. Reports in the early 1990s that dwarf mammoths survived to early historical times, on islands off the coast of Siberia, give force to such speculation. If dinosaurs found a similar haven in which they outlived the rest of their kind, then we think polar Gondwana, including southeastern Australia, is a likely place to look. SA

Patricia Vickers-Rich and **Thomas Hewitt Rich** collaborate on the study of fossils. Vickers-Rich holds a personal chair in paleontology at Monash University in Melbourne, Australia. She is interested in reconstructing ancient environments, especially those without modern analogues, and in analyzing rapid biotic change. Rich is curator of vertebrate paleontology at Museum Victoria in Melbourne. He conducts research on the evolutionary patterns of Mesozoic vertebrates, specializing in primitive mammals and ornithischian dinosaurs. The Riches received undergraduate degrees in paleontology from the University of California, Berkeley, and doctorates in geology from Columbia University. They live near Melbourne and have two children.

MORE TO EXPLORE

Dinosaurs of Darkness. Thomas H. Rich and Patricia Vickers-Rich. Indiana University Press, 2000.

A Century of Australian Dinosaurs. Thomas H. Rich and Patricia Vickers-Rich. Queen Victoria Museum and Art Gallery and the Monash Science Center, 2003.

The Artist and the Scientists: Bringing Prehistory to Life. Peter Trusler, Patricia Vickers-Rich and Thomas H. Rich. Cambridge University Press, 2010.

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STEVE MORTON (*photograph*)

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DOMINANT PREDATOR in Late Cretaceous Alaska was *Troodon*. This two- to three-meter-long dinosaur viewed the world through unusually large eyes—a feature that may have contributed to its hunting success during the long months of twilight above the Arctic Circle.

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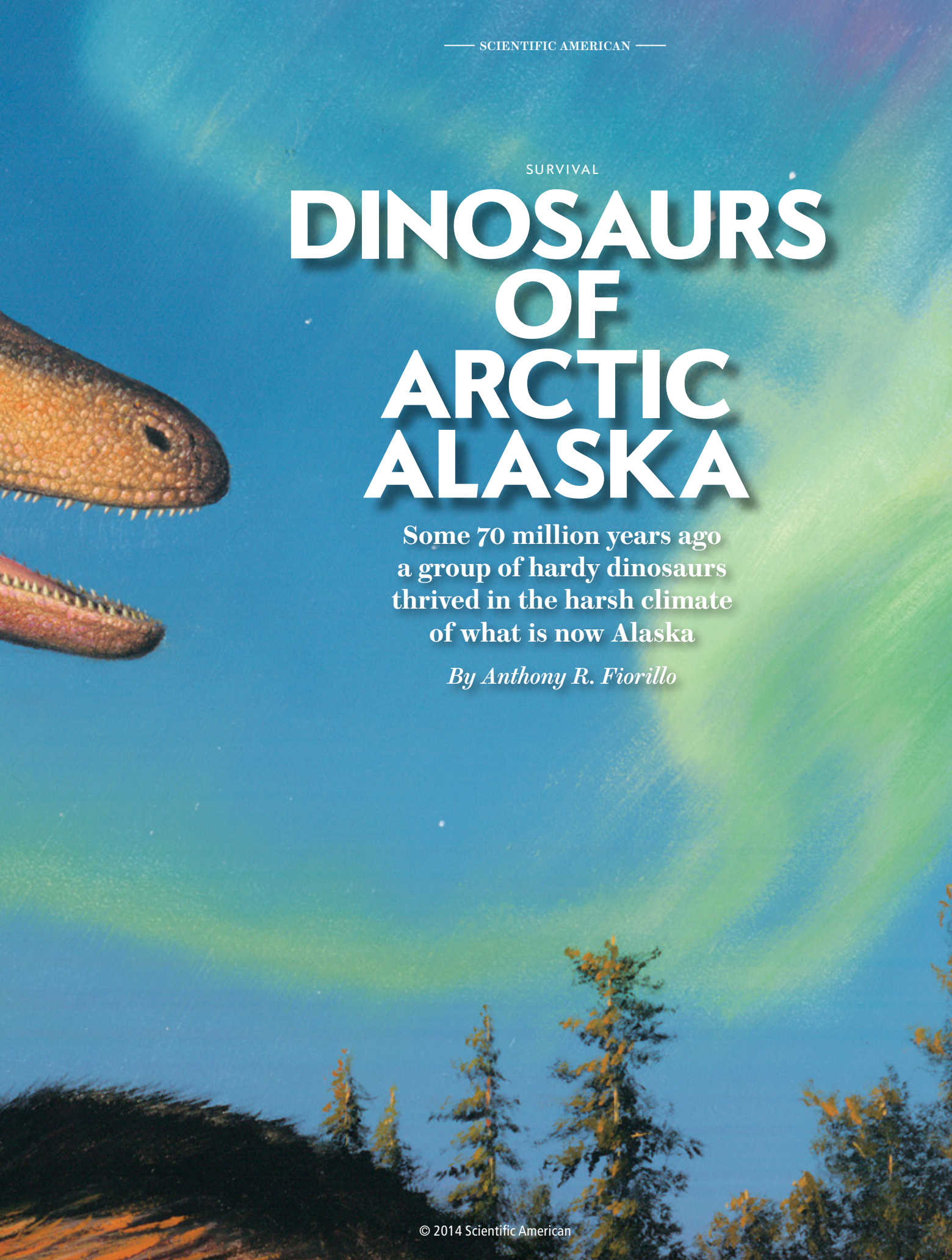

SURVIVAL

DINOSAURS OF ARCTIC ALASKA

Some 70 million years ago a group of hardy dinosaurs thrived in the harsh climate of what is now Alaska

By Anthony R. Fiorillo

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A FEW MORE SWEEPS WITH THE WHISK BROOM, AND THE BONE AT MY KNEES suddenly came into focus. I was looking at the snout of a *Pachyrhinosaurus,* a particularly odd horned dinosaur, a rare relative of *Triceratops.* It was not the first, or even the second, fossil of this creature found in Alaska, but I could already see parts of this skull that were not preserved on the other specimens. Continued excavation at the site—with picks and shovels supplementing our whisk brooms—yielded the bones and teeth of at least three other dinosaur species. It would take another trip for me to realize we were also crawling over 10 more skulls of *Pachyrhinosaurus*. Most individuals were close in age and had probably died together in a flood or other catastrophe. This grouping was the first evidence that horned dinosaurs north of the Arctic Circle behaved gregariously.

I had come to this remote spot on a bluff overlooking the Colville River in the summer of 2006 with colleagues from the Perot Museum of Nature and Science and Southern Methodist University to excavate the skull of a *Pachyrhinosaurus* I had found in 2002. We undertook a massive excavation from 2005 to 2007.

The genus name *Pachyrhinosaurus* means "thick-nosed lizard." After years of careful laboratory work and study of the new specimens gathered during our excavations, we discovered that our horned dinosaur was a new species of the genus. We named the Arctic horned dinosaur *Pachyrhinosaurus perotorum,* after the primary benefactors of our museum, the Ross and Margot Perot family.

No one has yet excavated a complete dinosaur skeleton from this site or anywhere else in Alaska. We have been able to identify from partial skeletons, isolated bones, teeth and fossil footprints several types of dinosaurs (including birds) and other fossil vertebrates that lived as contemporaries in the far north [*see illustration on pages 58 and 59*]. All these animals are from the Cretaceous period, which lasted from 145 million to 66 million years ago, but our animals date from just 70 million to 69 million years ago, some three to four million years before the famous mass demise of the planet's dinosaurs. Our work is ongoing, but we have begun to fill in some details about what kind of dinosaurs lived at the top of the world millions of years ago and how they survived there.

THE CAST OF CHARACTERS

SOME SPECIES ATE PLANTS, whereas others, called theropods, preyed on the plant eaters and other creatures. By far the most abundant dinosaurs of Alaska were the duck-billed dinosaurs, which are known from both fossil bones and footprints. Hadrosaurs—large, plant-eating dinosaurs—also go by the name "duckbills" because they had broad, flat mouths; in contrast to ducks, however, they had hundreds of teeth that could grind the tough plants they fed on. They could stand on their back legs to reach overhead foliage, although they traveled on all fours, probably in a rocking gait, because their rear legs were longer than their front. *Edmontosaurus* earns the prize for the hadrosaur that is best known from bones and so is the best characterized. Weighing in at between 1,400 and 1,800 kilograms, *Edmontosaurus* ranks among the largest of the hadrosaurs found in North America. These hadrosaurs comprise about 80 percent of the herbivorous dinosaurs found in Alaska. Like other hadrosaurs, *Edmontosaurus* were social animals that gathered in herds, as evinced by their bones, which have been found in piles at various places in northern Alaska as though groups of them had died in a flash flood.

Since 2002, Alaska has proved to be a paleontological candy store; it seems as though there are new discoveries in new places every year. Thanks to continued support from the National Park Service, we now have a robust record of dinosaurs from parks around Alaska, including from Aniakchak National Monument,

IN BRIEF

Over the past 30 years paleontologists have discovered that Alaska was home to large populations of various dinosaurs (including a diversity of birds). **Duck-billed** and horned dinosaurs are among the species that lived in the region 70 million to 69 million years ago. **These creatures** must have had adaptations that allowed them to survive the extended months of darkness and cold; clues about these special characteristics are beginning to emerge.

PRECEDING PAGES: LARRY FELDER

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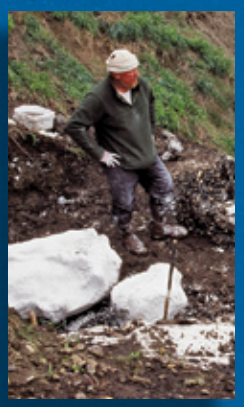
Dinosaurs at the Top of the World

During the Cretaceous period, some 70 million years ago, continental landmasses (*orange regions in inset at bottom left*) occasionally included a bridge of land, or isthmus, across what is today the Bering Strait. Dinosaurs probably walked across this stretch of land from Asia to North America. Some settled in the far north; others headed south.

In present-day Alaska the author and other paleontologists search for fossil remains at sites such as Kikak-Tegoseak Quarry (*top right*), where they found skulls of horned *Pachyrhinosaurus* dinosaurs. One of the richest sites for bones is Liscomb Bone Bed, where finds include a group of juvenile duck-billed dinosaurs, or hadrosaurs (*bones at bottom right*), which probably died together, perhaps in a flash flood. Footprints of a small predatory dinosaur (*middle right*) from a nearby site on the Kaolak River appear white because of a silicone compound that is used to mold the ancient imprints. Another footprint (bottom center)—from the Aniakchak National Monument in southern Alaska—was molded and contoured to allow the scientists to identify and study it.



Kikak-Tegoseak Quarry

Dinosaur footprints near Kaolak River

Landmasses 70 million years ago

Hadrosaur footprint from Aniakchak National Monument, with contoured cast

Lower leg bones from juvenile hadrosaurs at Liscomb Bone Bed

EDWARD BELL AND TOMMY MOORMAN (*maps*); SOURCE: C. R. SCOTESE. COPYRIGHT © 2003 PALEOMAP PROJECT (*landmass data*); ANTHONY R. FIORILLO (*photographs*)

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Wrangell–St. Elias National Park, Yukon–Charley Rivers National Preserve and, most notably, Denali National Park—where the fossil record includes a remarkable diversity of birds. Together the finds in this region give us insights into biodiversity and biological adaptation in an ancient, high-latitude terrestrial ecosystem.

Alaska was not the only surprising home to dinosaurs. Other researchers, such as Patricia Vickers-Rich of Monash University and Thomas Hewitt Rich of Museum Victoria, have uncovered fragmentary remains of dinosaurs that lived near the South Pole during a much earlier period [see "Dinosaurs of Polar Australia," on page 46].

HOW DID THEY GET THERE?

HOW DID DINOSAURS find themselves at the planet's northern extreme? More than likely they came from Asia because ancestral forms of almost all the Cretaceous dinosaur families found in North America existed in Asia. Most paleontologists believe that some of these dinosaurs migrated across a land bridge exposed by a drop in sea level where the Bering Sea sits today [*see box on preceding page*]. The configuration of continental plates during the Cretaceous suggests that the earliest these plates were in position to serve as a land bridge was approximately 120 million years ago. Some of the immigrants probably just stayed in the far north because the environment there supplied their needs; others headed south. One species, though, seems to have taken a different route. *Alamosaurus,* a plant-eating dinosaur roughly 20 meters in length, apparently arrived by a southerly migration path—remains of its ancestors are found on the continents of South America and Africa.

Alaska is built of enormous geologic blocks, some of which orig-

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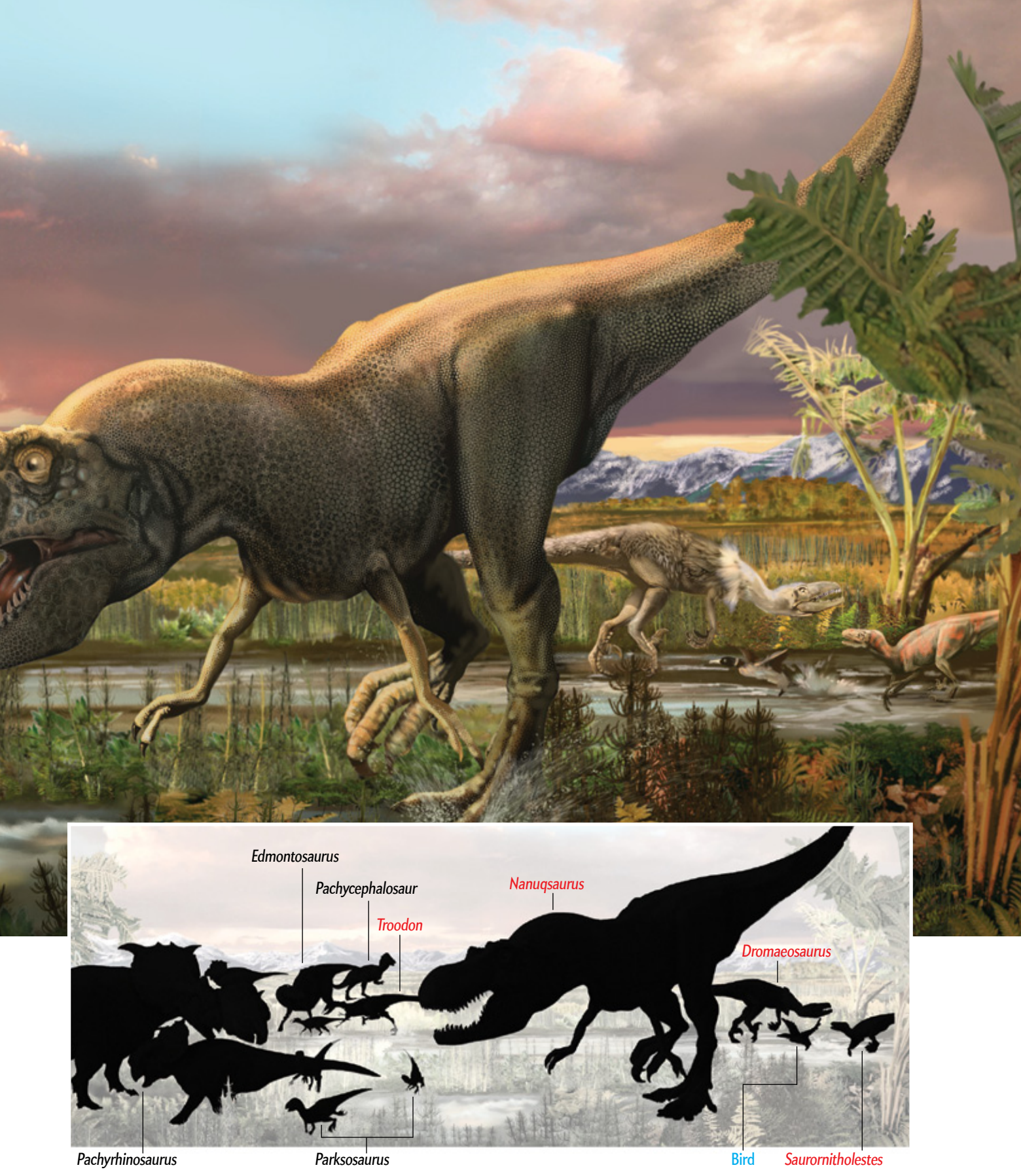

KAREN CARR

ALASKA circa 70 million years ago. Four plant-eating species (*black labels above*) and four predators (*red labels*) foraged and hunted in the ancient landscape dotted with bald cypress and metasequoia-type trees. The mountains rising in the background are the ancestral Brooks Range. At the lower right a ducklike bird, based on tracks found in Denali National Park, flees the predatory *Saurornitholestes*.

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FIELDWORK

Serendipity in Storage

In 1961 the late Robert L. Liscomb, a geologist who worked for Shell Oil Company, found a handful of bones of a duck-billed dinosaur, *Edmontosaurus.* These bones are extraordinarily well preserved, but because Liscomb and his colleagues were not vertebrate paleontologists, they identified the bones as much more recent fossil mammal bones. Liscomb died the following year in a rockslide, and his discoveries languished in storage.

In the mid-1980s Henry Roehler and Gary Stricker of the U.S. Geological Survey reported various fragmentary dinosaurian remains, such as fossil skin impressions, from northwestern Alaska. Soon thereafter, the USGS came into possession of the original Liscomb collection of bones; Charles A. Repenning properly recognized that they were dinosaurs, and USGS field crews located the area where Liscomb had done his initial work.

In the late 1980s the University of California Museum of Paleontology and the University of Alaska Museum continued the fieldwork in this remote area, turning up finds that hinted at abundant remains of dinosaurs and other animals. Because of my interest in northern high-latitude dinosaur ecosystems, I was invited to participate in the project in 1998, and I have continued to make research trips to Alaska every year since, most recently expanding the search into several of the state's national parks.

—A.R.F.

BURLAP in hand, the author makes field jackets for bones at Kikak-Tegoseak Quarry.

inated far from their present location. During the Cretaceous, however, many of these blocks of land were near their current latitudinal position or higher. Thus, the dinosaur fossils found in Alaska were not posthumously hijacked from distant climes and brought there on moving plates: they lived in the high latitudes during the Cretaceous. Did they stay there all year? And if so, how did they manage it?

COPING WITH COLD

ANSWERING THAT QUESTION requires knowledge of the climate in Alaska some 70 million years ago. True, the world was warmer then, but the climate in the high-latitude lands was still challenging, with cold, snowy winters and several months of darkness. Climatological data from fossil pollen, leaves and wood indicate that the Cretaceous forests of northern Alaska consisted of a mixed canopy that included deciduous conifers with an understory of flowering plants, ferns and horsetails. Today mixed coniferous forests occupy a wide but well-defined range of climates with mean annual temperatures from three to 13 degrees Celsius (37 to 55 degrees Fahrenheit), suggesting that the average yearly temperature for northern Alaska during the Cretaceous was similar.

One of the striking aspects of the modern Arctic is the angle of sunlight and the length of the day—commonly, though mistakenly, referred to as six months of daylight and six months of night. In actuality, north of the Arctic Circle, darkness occupies a longer and longer part of each day until the late-December winter solstice, when the sun does not rise. During the Cretaceous, northern Alaska was even farther north than it is today, and so the dinosaurs that lived there would have needed mechanisms to cope with both the cold and the dark.

We do not know the full explanation of how they survived. It seems unlikely that a 10-meter-long (35-foot-long) hadrosaur dug a hole in the ground and went into hibernation. But during times of environmental stress, some animals can lower their metabolic rates enough to reduce their need for food; perhaps Arctic dinosaurs did something similar without reaching an official state of hibernation.

In trying to explain how hadrosaurs survived the harsh climate, Nicholas Hotton III of the Smithsonian Institution suggested that in winter they migrated thousands of kilometers to find forage, warmer temperatures and better light conditions. Subsequently, other researchers used modern caribou as an example of a long-distance migrant to support such theories about the migration of Arctic dinosaurs.

To investigate the likelihood that hadrosaurs migrated, Roland Gangloff, now a professor emeritus at the University of Alaska, and I decided to see how well caribou work as an analogy for hadrosaurs. First we compared the body sizes of adults and juveniles in three Arctic herds of caribou. We discovered that juvenile caribou reach 80 to 85 percent of adult length and 53 to 74 percent of adult mass by the onset of migration.

Then we looked at the hadrosaur fossils. The cell structure of the bones clearly shows that the small hadrosaurs were juveniles at least one year old—not some form of a dwarf, high-latitude population. The lengths of the bones of the juveniles indicate that they were 27 to 37 percent of adult size and an estimated 11 percent of adult mass.

CHRISTOPHER STRGANAC

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The juvenile hadrosaurs, then, were relatively much smaller at one year of age than juvenile caribou are at the time of their seasonal migration. Therefore, on simple biomechanical grounds, it seems unlikely that hadrosaurs of the Arctic migrated great distances. We have not, however, discovered nests or eggs, which would of course clinch the argument that dinosaurs remained year-round at these high latitudes.

But if they stayed year-round, what did they eat during the cold winter months? We presume that the predators continued to eat meat because the patterns of wear on their teeth suggest no change in diet during the year.

We do not know exactly what the herbivorous dinosaurs ate. *Edmontosaurus* offers an opportunity to speculate, however, because it had a range from northern Alaska all the way south to West Texas. Today another herbivorous vertebrate—the mountain sheep of North America—has a comparable range. The diets of southern-latitude sheep are more restricted than those of northern-latitude sheep, probably because they have more resources available to them and can afford to be more particular. Analogously, northern individuals of *Edmontosaurus* may well have had a more generalized diet than their southern counterparts.

U.S. ARMY CHINOOK helicopter lifts a plaster jacket containing parts of three *Pachyrhinosaurus* skulls from Kikak-Tegoseak Quarry. Out on a training mission,the helicopter's crew came to the aid of the scientists in removing the heavy load of fossils.

If the dinosaurs did not migrate, then presumably they would show adaptations supportive of year-round life in the high latitudes. *Troodon* provides the clearest example at the moment. This small, meat-eating dinosaur, known mainly from its teeth, is rare in more southern places, such as Alberta, Montana and Texas. In contrast, isolated teeth of this animal are very common in Alaska, which suggests that the population was large and widespread. What sets *Troodon*—at any latitude—apart from other predatory dinosaurs is its exceptionally large eyes. Among modern animals, proportionately large eyes tend to be an adaptation for living in low light conditions. *Troodon* may have been preadapted to the physical constraints of the high-latitude environment, which gave it a competitive advantage and set it on the path to become the most abundant predator of the northern ecosystem.

If *Troodon* was well adapted to the low light of Arctic winters, one might wonder how it could function during the long periods of daylight in warmer months. The forest might have provided refuge then. Anyone who has walked through even a modestly dense forest can appreciate how much lower the light level is in the woods than it is in an open field. In such an environment *Troodon*'s large eyes would have continued to make it a fearsome predator.

We cannot confirm the size of the eyes of the other dinosaurs that lived in Alaska, because those parts of the skulls are only fragmentary or the bones are still being prepared for study. Although the dinosaurs described from southern Australia by Tom and Pat Rich are much older and very different, the Riches did note a pattern of increased orbital diameters for some dinosaurs.

Interestingly, *Troodon* in the Arctic were nearly twice the size of *Troodon* found in more southern locations. This difference contrasts sharply with the pattern discerned from measuring the bones of herbivorous dinosaurs of the North Slope, which fall well within the size range of those found in lower latitudes. It could be that *Troodon*'s large eyes gave it a competitive advantage, eventually allowing it to become the top predator and to increase in size. Observers have reported a similar phenomenon in modern ecosystems: where wolves have been removed, coyotes have sometimes achieved larger body sizes.

LONE SURVIVORS?

CLEARLY, MANY QUESTIONS remain to be answered about these extraordinary creatures. One of the most fascinating is whether they might have survived beyond the catastrophe that killed off the dinosaurs in other parts of the world at the end of the Cretaceous period.

Most paleontologists believe that a collision between the earth and a large asteroid drove the dinosaurs to extinction. The most likely location for the impact is the Chicxulub crater in Mexico. To study the far-reaching effects of such an impact, ideally one would look to a place far removed from the site, a place such as Alaska. Unfortunately, we have not found any fossils of dinosaurs in Alaska at just the right time to have a direct bearing on the question of whether dinosaurs died out abruptly or gradually. Fossil pollen data, however, offer tantalizing evidence that sections of rocks on the North Slope and elsewhere in Alaska are the right age to shed light on the extinction if they prove to contain fossils of fauna in addition to pollen. The possibility adds even more impetus to our search for ancient bones. We have just scratched the surface. SA

Anthony R. Fiorillo, as far back as he can remember, has wanted to do only one of two things professionally: play center field for the New York Yankees or study dinosaurs. Much to the detriment of his parents' retirement plans, he studies dinosaurs. Fiorillo completed his Ph.D. in vertebrate paleontology at the University of Pennsylvania in 1989. In 1995, after stints at the Carnegie Museum of Natural History and the Museum of Paleontology at the University of California, Berkeley, he went to Dallas, where he is curator of earth sciences at the Dallas Museum of Natural History and an adjunct associate professor at Southern Methodist University.

MORE TO EXPLORE

Dinosaurs: The Science behind the Stories. J. G. Scotchmoor, D. A. Springer, B. H. Breithaupt and A. R. Fiorillo. American Geological Institute, 2002.

Bird Tracks from the Upper Cretaceous Cantwell Formation of Denali National Park, Alaska, USA: A New Perspective on Ancient Northern Polar Vertebrate Biodiversity. Anthony R. Fiorillo, Stephen T. Hasiotis, Yoshitsugu Kobayashi, Brent H. Breithaupt and Paul J. McCarthy in *Journal of Systematic Palaeontology,* Vol. 9, No. 1, pages 33–49; 2011.

A New Maastrichtian Species of the Centrosaurine Ceratopsid *Pachyrhinosaurus* from the North Slope of Alaska. Anthony R. Fiorillo and Ronald S. Tykoski in *Acta Palaeontologica Polonica,* Vol. 57, No. 3, pages 561–573; 2012.

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ANTHONY R. FIORILLO

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TAPHONOMY

A 70-MILLION-YEAR-OLD MURDER MYSTERY

The case was cold, but critical clues pointed to a killer's identity in ancient Madagascar

By Raymond R. Rogers and David W. Krause

ONE BODY RESTS ON ITS LEFT SIDE, HEAD AND NECK PULLED BACK TOWARD the pelvis—a classic death pose. The arms and legs are still in their anatomically correct positions, but closer inspection reveals that bones of the hands and feet are dislocated, although most parts are present and accounted for. The skull, too, is somewhat disjointed, and here again the component pieces lie near one another. Curiously, the tip of the tail is missing altogether. Nearby rest more corpses in markedly different states of preservation and disarray. Some are still largely intact, others represented by only a skull, a shoulder blade, a single limb bone. Did the unfortunate creatures die here, or were they brought together after their demise? Did they all perish at the same instant, or did their deaths transpire over time? And what killed them?

IN BRIEF

A mass grave in northwestern Madagascar contains the remains of dinosaurs that died about 70 million years ago, during the Late Cretaceous.

Researchers studied the bones for clues about what had killed so many dinosaurs of different sizes, ages and species.

The evidence suggests that the animals perished over a prolonged period, probably as they congregated around parched riverbeds.

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LARGE, MEAT-EATING DINOSAUR *Majungasaurus crenatissimus* (*above*) met an untimely death some 70 million years ago, near the end of the Cretaceous period, in what is now northwestern Madagascar.

RAYMOND R. ROGERS

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Evidence Collection

Members of the authors' team carefully excavated the remains of dinosaurs of various species from a site in semiarid grasslands near the village of Berivotra in what is now northwestern Madagascar (*1*). Packed in plaster (*2*), the bones were transported to the U.S., where the researchers studied the fossils in detail for clues about how these animals lived and died. The remains included the jaw of an *M. crenatissimus,* which used its serrated teeth to slice through flesh (*3*).

Our team of Malagasy and American paleontologists and geologists started asking such questions as soon as we discovered the mass grave in the summer of 2005 in the ancient sediments of northwestern Madagascar, an island whose Venetian-red soils inspired its nickname, the Great Red Island. We turned up some intriguing information as we searched for the answers, but how we went about the task is perhaps as interesting as what we found.

Before doing anything, we named the site, designating it MAD05-42 to indicate the year it was found and its sequence in the discovery of fossil localities in this area. The second task was identifying the dead, and based on our discoveries elsewhere in the region, we quickly discerned that most of the remains were dinosaurs of various species.

This dinosaur burial ground is not unique for northwestern Madagascar. It matches a pattern we have seen repeatedly over more than a decade of geologic investigation in the semiarid grasslands near the remote village of Berivotra. There we have uncovered layer on layer of mass death, with the remains of animals big and small, young and old, entombed together in spectacular bone beds. And so as we worked to uncover what killed the animals in MAD05-42, we also could not help but wonder why we find so many bone beds here and why they are so beautifully preserved.

OPENING A VERY COLD CASE

WE WERE MILLIONS OF YEARS too late to use most of the tools of modern-day coroners. To tease out the clues hidden in the bones and rock, we had to turn to geologic dating techniques and to the field of inquiry known as taphonomy, which explores the fate of organic remains as they cross from the living world to the dead.

After naming the site, we disinterred the bones from the rocks in which they were embedded. We started with shovels and rock hammers to remove the overlying sediment, then moved on to dental picks and fine brushes to expose the bones themselves. We took great care not to damage the fragile bone surfaces. Once we fully exposed the skeletal remains, we mapped and photographed them exactly where we found them to record any significant spatial relationships. We next soaked the delicate bones with consolidating glues and carefully jacketed them in protective coats of burlap and plaster. After the plaster set, we catalogued the bones and packed them for the long journey to our laboratories in the U.S., where lat-

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FINDINGS

More Mass Death

One of the first sites discovered, MAD93-18, reveals the recurrent nature of mass mortality in ancient Madagascar more dramatically than any other site. MAD93-18 has three discrete deathbeds stacked one on top of the other. Excavations there uncovered the skeletal remains of many animals new to science, including a primitive bird, *Rahonavis ostromi* (*1*), which had small, fragile bones. The site also produced nearly complete skeletons of the large sauropod *Rapetosaurus* (*2* and *3*).

1

2

3

er we painstakingly removed any remaining sediment and studied the bones in detail, looking in particular for any marks on the surfaces that might reveal the killer's identity.

At the site we determined that the dead were preserved in a distinctive body of sedimentary rock known as the Maevarano Formation, situated a few tens of meters below rocks laid down at the Cretaceous-Paleogene boundary—the time, 66 million years ago, that all dinosaurs (apart from birds) and many other creatures suffered extinction on a global scale. The deathbed lay 44.5 meters underneath the mass extinction horizon and 14.5 meters below the local top of the Maevarano Formation. Measuring the radioactive decay of minerals from volcanic rocks in the layers under the formation yielded ages of approximately 88 million years. Marine sediments above and interbedded with the formation, laid down by seas that ebbed and flowed along the western shores of the island, contained seashells and tiny skeletons of single-celled microorganisms dated from other sites to near the end, but not the very end, of the Cretaceous period. All the temporal evidence thus indicates that the deaths occurred approximately 70 million years ago. Whatever killed the dinosaurs in quarry MAD05-42 was unrelated to the great global extinction that took place several million years later.

Taphonomy advanced our inquiry as well. Taphonomic study examines bone modification (were the bones burned, broken or bitten?), carcass disturbance (dismemberment and selective removal of body parts by scavengers or predators), and burial history (how the bodies were buried and what happened to them after burial). The study of fossilization processes—essentially, what turns bone into stone—also falls within the realm of this science.

When we considered the dead in quarry MAD05-42 from a taphonomic perspective, we could tell that they perished over a prolonged period, perhaps weeks or months, because their corpses revealed variable postmortem histories. For example, some carcasses were largely intact, and others were dismembered and scattered widely, which would not have happened instantaneously. In addition, some bones were in exquisite condition, whereas others showed evidence of advanced weathering and surface degradation. When the animals in an ancient bone bed have died at different times, we describe the site as "time-averaged" and use taphonomic clues to assess the amount of time between the first death

CATHERINE FORSTER *Stony Brook University (1);* RAYMOND R. ROGERS *(2);* DESIRÉ RANDRIANARISTA *Centre Valbio (International Training Center for the Study of Biodiversity) (3)*

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SIGNS

Dining on the Dead

Widespread death in Madagascar during the Late Cretaceous provided a smorgasbord for those that fed on the dead. Necrophagy, the act of consuming corpses or carrion, is a niche that must be filled if biological recycling is to proceed efficiently, and modern practitioners range from bacteria to large-bodied vertebrates. Along with our colleague Eric M. Roberts, who accompanied us to Madagascar more than a decade ago as an undergraduate (and is now a senior lecturer at James Cook University in Australia), we have found traces of necrophagous insect activity in the dinosaur bones of Madagascar: centimeter-long oval pits, usually in what had been spongy tissue inside the bones. These pits are signs that adult beetles infested the corpses, fed on the carrion and then laid their eggs nearby. After hatching, the larvae fed as well and used their robust mandibles to excavate the pits, which served as pupation chambers.

Insects were not the only creatures feeding on the dead. Analysis of bite marks has yielded irrefutable evidence that dinosaurs also dined here. Working in collaboration with Kristina A. Curry Rogers of Macalester College, we have documented tooth marks of the seven-meter-long theropod *Majungasaurus* on a selection of bones from at least three separate bone beds. Comparing the shape and size of the tooth marks with the jaws and teeth of various carnivores, we have been able to rule out all the other sharp-toothed suspects.

A few of the bitten bones in our sample belong to *Rapetosaurus,* a previously unknown long-necked sauropod dinosaur that Curry Rogers described as part of her dissertation work at Stony Brook University. Yet the vast majority of tooth-marked bones, primarily ribs and vertebrae, belong to *Majungasaurus* itself. Cannibalism as an ecological strategy is not at all uncommon among living animals, and it certainly should not be unexpected among dinosaurs. Unearthing the evidence to prove it, however, has been another matter, and in the bone beds of Madagascar we have documented the only well-substantiated case of cannibalism among dinosaurs. Unfortunately, the bite-mark evidence does not definitively disclose whether *Majungasaurus* actually killed the individuals it dined on—and thus practiced predation on its own species—or simply opportunistically scavenged their remains. —*R.R.R.* and *D.W.K.*

OVAL PITS in the dinosaur bones (***photograph***) are signs that carrion beetles infested the corpses, fed on the flesh and then laid their eggs (***illustration at right***).

RAYMOND R. ROGERS (*left*); RAÚL MARTIN (*right*)

DINOSAURS!

and the last. Although we cannot determine exactly how much time transpired in the formation of this particular deathbed, we do know that death did not come at the same instant for the animals entombed here.

SCENE OF THE CRIME

THE GEOLOGIC HISTORY of the Madagascar landmass also provided important clues about what killed these dinosaurs. At the onset of the Mesozoic era (252 million years ago), Madagascar rested in the heart of Gondwana (the southern half of the supercontinent Pangaea), sandwiched between Africa and India, with Antarctica near its southern tip. Tectonic activity soon rearranged lithospheric plates on a massive scale, and by the Late Jurassic (160 million years ago), Madagascar had rifted away from Africa and was moving southward, with India in tow. By 88 million years ago, during the Late Cretaceous, Madagascar had resutured to the African plate, albeit about 400 kilometers distant from the mainland, and the Indian subcontinent and Antarctica had rifted away, leaving the world's fourth largest island isolated in the Indian Ocean.

After reuniting with the African plate, Madagascar shifted northward toward its present location in the Southern Hemisphere tropics. But when the deaths under investigation transpired, some 70 million years ago, northern Madagascar was positioned near 30 degrees south latitude—still far from the Tropic of Capricorn (which now passes through *southern* Madagascar) and arguably well within the influence of subtropical weather patterns [*see box on page 69*]. Today major deserts and semideserts occur in swaths between 15 and 35 degrees north and south of the equator. These arid belts reflect large-scale atmospheric circulation patterns (known as the Hadley cell) that drive masses of hot, dry air down

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1

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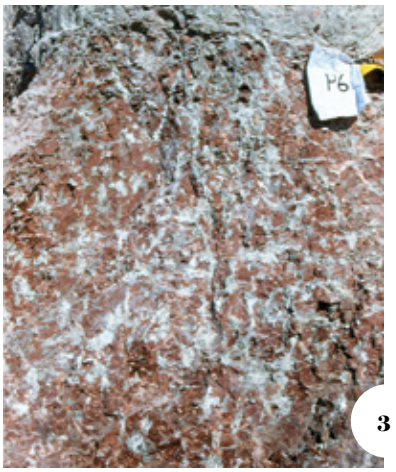

3

ANCIENT SOILS and rocks present convincing evidence of a semiarid climate during the Late Cretaceous. Vertically oriented root casts (*3*) indicate that plants had adapted to dry conditions by seeking deep sources of moisture. Many of the relic roots also reveal clumps of calcium carbonate, which tend to form in arid regions. Other sediments, laid down in sandy rivers (*1* and *2*), indicate that water flow varied dramatically. When the rivers were flowing, currents drove dunes downstream, resulting in stacked sets of inclined layering (*2*). Dinosaurs and many other animals visited the shallow rivers in search of nourishment—in fact, the bones of quarry MAD05-42 lie in one of these ancient channels.

to the earth after they have relinquished their moisture near the equator. The high-pressure zones that result from the descending air cells tend to keep rainfall at bay most of the time, but when rain does come, it can be intense.

Rocks of the Maevarano Formation present convincing evidence of a semiarid and seasonal climate during the Late Cretaceous. Most telling are the red oxidized paleosols (ancient soils), which contain beautifully preserved, vertically oriented casts of roots. Vertical roots are common today where plants have adapted to dry conditions by seeking ever deeper sources of moisture and nutrients. Furthermore, many of the relic roots of the Maevarano Formation are encrusted with calcium carbonate or interspersed with irregular clumps of this mineral that are called carbonate nodules. In the modern world, oxidized soils enriched in calcium carbonate tend to occur in semiarid to arid regions, where evaporation and transpiration limit the effects of precipitation.

Other sediments of this ancient terrain were laid down in shallow, sandy rivers. These, too, provide telling evidence of a subtropical history, with clear indication that the flow of water fluctuated dramatically and probably seasonally. When the rivers were flowing, currents drove ripples and dunes downstream, resulting in stacked sets of inclined layering that geologists refer to as cross-stratification.

Dinosaurs and many other animals no doubt frequented these rivers in search of water, nourishment or refuge. Indeed, the bones in quarry MAD05-42 are scattered in one of these ancient river channels. Part of the time the rivers were dry; at other times they roiled with thick milk shake–like slurries of mud and sand. We will return to these slurries—they play an important role in our story.

IDENTIFYING A KILLER

A LONE ANIMAL can meet its end in many ways—perhaps too many, if the goal is to positively identify a killer in the fossil record. But the options diminish significantly in cases of mass death, such as those in the Maevarano Formation. For help in narrowing the possibilities down to one, we looked again to taphonomy. The bone beds of Madagascar generally preserve the remains of more than one type of animal, be it multiple species of dinosaurs, as in MAD05-42, or a more diverse array, as in quarry MAD93-18 [*see box on page 65*], which has yielded the skeletal remains of fishes, turtles, snakes, crocodiles, three different types of nonavian dinosaurs, birds and mammals. This killer was indiscriminate, paying no attention to size, age, taxonomy or habitat—a fact that tends to exclude a predator, such as a meat-eating dinosaur or crocodile, because modern predators generally show at least some degree of prey selection.

Nor is there any support for a disease-based scenario (it is difficult, though, to test for disease with fossilized bones). Because the creatures died at different times, we do not suspect dramatic instantaneous events such as earthquakes, floods or fire. Whatever killed the animals acted over time and struck victims individually after they had arrived at the river under their own volition. We

RAYMOND R. ROGERS

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DROUGHT was the killer. Animals congregated in the parched riverbeds, where they perished as food and water disappeared. The large dinosaur *Majungasaurus* fed on *Rapetosaurus* (*foreground*) as well as on its own kind (*far left*). Birds (*Rahonavis*) also scavenged the remains. The immediate cause of death could have been dehydration, heat stress, malnutrition, even poisoning, as the stagnant water turned toxic. Other carnivorous animals and insects feasted on the carcasses until they, too, met their end when torrential rains triggered mudflows that encased the dead and dying, preserving their remains for 70 million years.

also have irrefutable evidence that the killer struck repeatedly in different locales but with the same basic modus operandi. These animals were not dropped in their tracks during one bad day in the Late Cretaceous—there were many bad days.

When all the evidence is brought to bear, we can confidently pinpoint one killer: drought. The opportunity certainly existed; this was a subtropical ecosystem with clear indications of aridity and seasonality. Moreover, we can see that animals congregated in the desiccating riverbeds, probably around remaining pools of water, where again and again they perished as good drinking water and nourishment disappeared. Today lethal droughts, especially in parts of Africa and interior Australia, prompt animals to gather around remaining resources. During an extended drought, thousands of animals can succumb at the site of their last hope for a drink, and their bodies may accrue in localized "dead zones" over several years.

Studies of modern drought-related mortality indicate that the unlucky animals preserved in the Maevarano bone beds could have ultimately died from any number of causes: dehydration, heat stress, malnutrition, perhaps even poisoning as their dwindling water supplies turned foul and noxious. In fact, we have some tantalizing evidence that algal blooms occurred in the stagnant pools of water that drew the animals together. Michael Zavada, a Cretaceous pollen expert from East Tennessee State University, has isolated tiny algal spores in the rocks associated with the bones; whether these spores represent telltale clues of toxic algal blooms, however, has yet to be confirmed.

But how were the animals' bodies preserved, many of them so exquisitely? Biological remains tend to fare poorly at the ground surface, where scavengers hold sway and the sun slowly but inexorably bleaches even the largest of bones until they splinter and eventually turn to dust. When long-term preservation in the

RAÚL MARTIN

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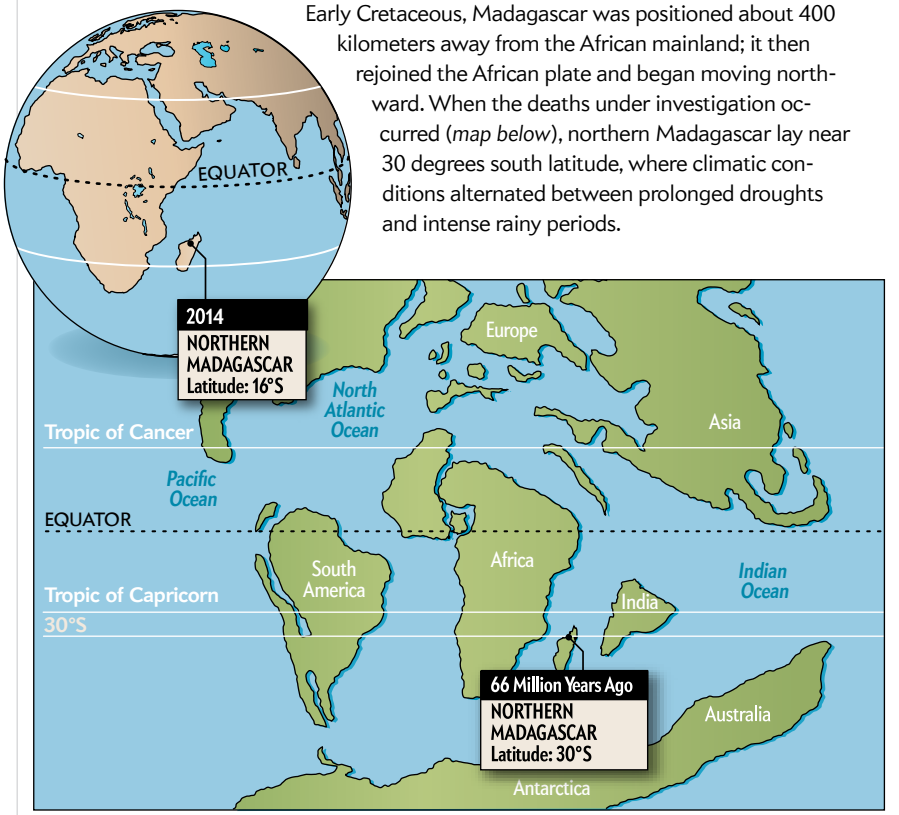
LUCY READING-IKKANDA

MAP

Geologic Evidence

The history of the Madagascar landmass provides clues about what killed so many animals there 70 million years ago. At the beginning of the Mesozoic era (252 million years ago), Madagascar rested in the heart of Gondwana. Tectonic activity rearranged the earth's lithospheric plates, and by 130 million years ago, in the Early Cretaceous, Madagascar was positioned about 400 kilometers away from the African mainland; it then rejoined the African plate and began moving northward. When the deaths under investigation occurred (*map below*), northern Madagascar lay near 30 degrees south latitude, where climatic conditions alternated between prolonged droughts and intense rainy periods.



fossil record is at stake, burial should occur as soon as possible after death. Indeed, it could be argued that from a fossil's perspective, rapid burial is the single most critical key to immortality.

Fortunately for those of us who study these fossils, a very efficient undertaker was operating in conjunction with the killer weather. The drought conditions that periodically spelled disaster in the parched riverbeds eventually had to come to an end, and when the rains returned, as they did with a vengeance, they triggered debris flows. Viscous slurries of green mud and sand mobilized by rain-induced erosion poured over the bones and encased them. The sedimentary characteristics of the burial beds reflect a special category of fluid flow in which turbulence is suppressed, and both water and sediment move en masse in an essentially plastic fashion. This type of mass flow, often known as a mudflow, is not uncommon today. The lethal mudslides in Guatemala in 2005, unleashed by the torrential rains of Hurricane Stan, are a modern example.

Again and again after the fatal droughts had taken their toll, thick beds of mud and sand flowed over the bodies and the scattered bones, whether they belonged to animals that had died minutes or months before, and effectively packaged them all together in a protective and permanent sedimentary tomb. It would be another 70 million years until the tombs were cracked open and the amazing stories within revealed. SA

Raymond R. Rogers and **David W. Krause** have excavated and investigated the spectacular bone beds of Madagascar since 1996. Rogers is a professor of geology at Macalester College and a research associate at the Field Museum in Chicago. He earned a Ph.D. in geology from the University of Chicago in 1995. Krause is Distinguished Service Professor in the department of anatomical sciences at Stony Brook University and a research associate at the Field Museum. He received a doctorate in geology from the University of Michigan at Ann Arbor in 1982. Krause's work in Madagascar, one of the world's poorest countries, led him to establish the Madagascar Ankizy Fund (www.ankizy.org), a nonprofit organization that builds schools and provides temporary clinics for children in remote areas of the island.

MORE TO EXPLORE

Monsters of Madagascar. John Flynn and David Krause in *National Geographic,* Vol. 198, No. 2, pages 44–57; August 2000.

Cannibalism in the Madagascan Dinosaur *Majungatholus atopus*. Raymond R. Rogers, David W. Krause and Kristina Curry Rogers in *Nature,* Vol. 422, pages 515–518; April 3, 2003.

Fine-Grained Debris Flows and Extraordinary Vertebrate Burials in the Late Cretaceous of Madagascar. Raymond R. Rogers in *Geology,* Vol. 33, No. 4, pages 297–300; April 2005.

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ORIGINS

WINGED VICTORY

Modern birds, long thought to have arisen only after the dinosaurs perished, turn out to have lived alongside them

By Gareth Dyke

DECEMBER IN MOSCOW, AND THE TEMPERature drops under 15 degrees below zero. The radiators in the bar have grown cold, so I sit in a thick coat and gloves, drinking vodka while I ponder the fossil birds. The year is 2001, and the now late Evgeny N. Kurochkin of the Russian Academy of Sciences and I have just spent hours at the paleontology museum as part of our effort to survey all the avian fossils ever collected in Mongolia by joint Soviet-Mongolian expeditions. Among the remains is a wing unearthed in the Gobi Desert in 1987. Compared with the spectacularly preserved dinosaur skeletons in the museum's collections, this tiny wing—its delicate bones jumbled and crushed—is decidedly unglamorous. But it offers a

SIDE BY SIDE: Based on fossil evidence from Antarctica, this artist's conception depicts *Vegavis*, an early modern bird, foraging alongside duck-billed dinosaurs in a marine estuary some 67 million years ago.

Illustration by Kazuhiko Sano

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strong hint that a widely held view of bird evolution is wrong.

More than 10,000 species of birds populate the earth today. Some are adapted to living far out on the open ocean, others eke out a living in arid deserts, and still others dwell atop snow-capped mountains. Indeed, of all the classes of land vertebrates, the one comprising birds is easily the most diverse. Evolutionary biologists long assumed that the ancestors of today's birds owed their success to the asteroid impact that wiped out the dinosaurs and many other land vertebrates around 66 million years ago. Their reasoning was simple: although birds had evolved before that catastrophe, anatomically modern varieties appeared in the fossil record only after that event. The dawning of ducks, cuckoos, hummingbirds and other modern forms—which together make up the neornithine ("new birds") lineage—seemed to be a classic case of an evolutionary radiation in response to the clearing out of ecological niches by an extinction event. In this case, the niches were those occupied by dinosaurs, the flying reptiles known as pterosaurs and archaic birds.

IT IS FUNNY TO THINK OF A ROBIN PERCHED ON THE BACK OF A *VELOCIRAPTOR* OR A DUCK PADDLING ALONGSIDE A *SPINOSAURUS.*

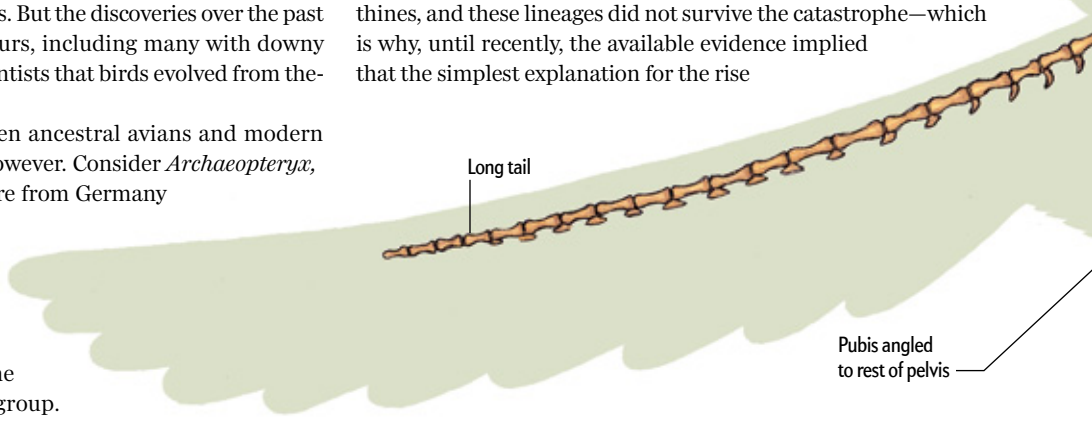
Over the past decade or so, however, mounting evidence from the fossil record—including that crushed wing—and from analyses of the DNA of living birds has revealed that neornithine birds probably diversified earlier than 66 million years ago. The findings have upended the traditional view of bird evolution—and sparked important new questions about how these animals soared to evolutionary heights.

EARLY BIRDS

BIRDS ARE ONE of just three groups of vertebrates ever to have evolved active, flapping flight. The other two are the ill-fated pterosaurs and the bats, which appeared much later and share the skies with birds to this day. For years paleontologists debated the origin of the earliest birds. One side argued that they evolved from small, meat-eating dinosaurs called theropods; the other contended that they evolved from earlier reptiles. But the discoveries over the past two decades of birdlike dinosaurs, including many with downy coats, have convinced most scientists that birds evolved from theropod dinosaurs.

Connecting the dots between ancestral avians and modern birds has proved far trickier, however. Consider *Archaeopteryx,* the 145-million-year-old creature from Germany that is the oldest known bird. *Archaeopteryx* preserves the earliest definitive evidence for wings with asymmetric feathers capable of generating the lift required for flight—one defining characteristic of the group. Yet it more closely resembles small-bodied dinosaurs such as *Velociraptor, Deinonychus, Anchiornis* and *Troodon* than modern birds. Like those dinosaurs, early birds such as *Archaeopteryx* and the more recently discovered *Jeholornis* from China and *Rahonavis* from Madagascar possessed long, bony tails, and some had sharp teeth, among other primitive traits. Neornithines, in contrast, lack those characteristics and exhibit a suite of advanced ones. These features include fully fused toe bones and fingerless wings, which reduce the weight of the skeleton, allowing more efficient flight, and highly flexible wrists and wings, which enhance maneuverability in the air. How and when the neornithines acquired these traits were impossible to determine, however, thanks to an absence of fossils documenting the transition.

This is not to say the fossil record lacked avian remains intermediate in age between the first birds and the postextinction neornithines. Clearly by more than 100 million years ago, in the Early Cretaceous, birds representing a wide range of flight adaptations and ecological specializations had evolved. Some flew on wings that were broad and wide; others had wings that were long and thin. Some lived in forests eating insects and fruit; others made their home along lakeshores or in the water and subsisted on fish. This incredible diversity persisted through the latest stages of the Cretaceous, 66 million years ago. In fact, along with my Dutch colleagues at the Maastricht Natural History Museum, I have described remains of toothed birds found just below the geologic horizon that marks the end-Cretaceous extinction event. But all the Cretaceous birds complete enough to classify belonged to lineages more ancient than neornithines, and these lineages did not survive the catastrophe—which is why, until recently, the available evidence implied that the simplest explanation for the rise



PATRICIA J. WYNNE

IN BRIEF

The descent of birds from small, meat-eating dinosaurs is by now established. Far less clear is the origin of anatomically modern birds.

The conventional fossil-based thinking is that modern birds arose only after the asteroid impact that claimed the dinosaurs 66 million years ago.

But molecular studies and a smattering of equivocal fossil finds have hinted that modern birds might have deeper roots. **Recently analyzed fossils** of ancient modern birds have confirmed this earlier origin, raising the question of why these birds, but not the archaic ones, survived the mass extinction.

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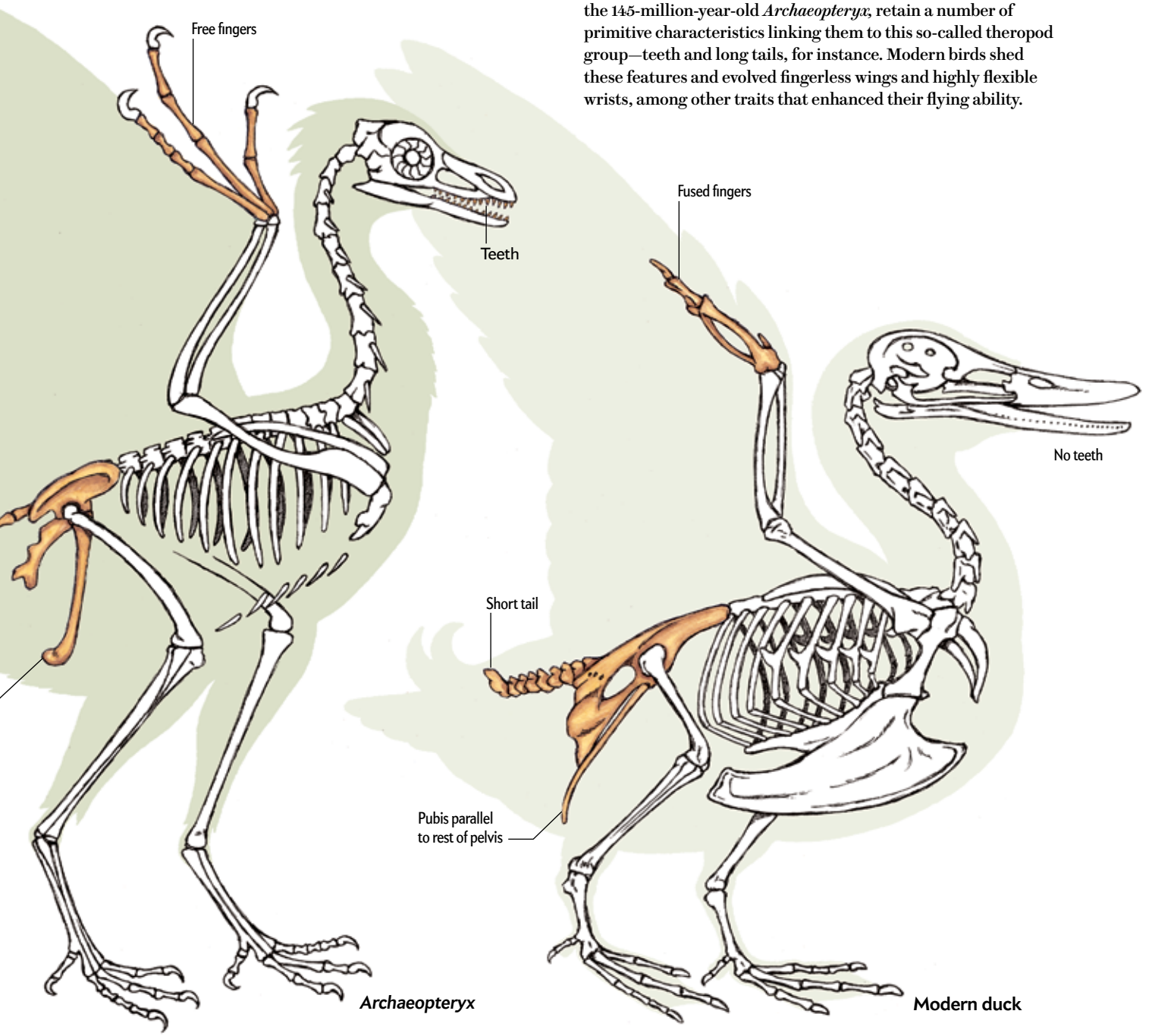
of modern birds was that they originated and radiated after the extinction event.

MOLECULAR CLUES

BY THE 1990S, while paleontologists were still looking for ancestral neornithines in the Cretaceous and coming up empty-handed, another method of reconstructing the evolutionary history of organisms—one that did not involve the fossil record—was gaining traction. Molecular biologists were sequencing the DNA of living organisms and comparing those sequences to estimate when two groups split from each other. They can make such estimates because certain parts of the genome mutate at a more or less constant rate, constituting the "ticking" of the so-called molecular clock.

Molecular biologists had long questioned the classical, fossil-based view of modern bird evolution. So they tackled the problem using their clock technique to estimate the divergence dates for major lineages of modern birds. Among the most significant splits is the one that occurred between the large, mostly flightless paleognaths (ostriches and emu and their kin) and the Galloanserae (which includes chickens and other members of the Galliformes group, as well as ducks and other members of the Anseriformes

BIRDS EVOLVED from small, carnivorous dinosaurs. Accordingly, some of the oldest known fossil birds, such as the 145-million-year-old *Archaeopteryx*, retain a number of primitive characteristics linking them to this so-called theropod group—teeth and long tails, for instance. Modern birds shed these features and evolved fingerless wings and highly flexible wrists, among other traits that enhanced their flying ability.



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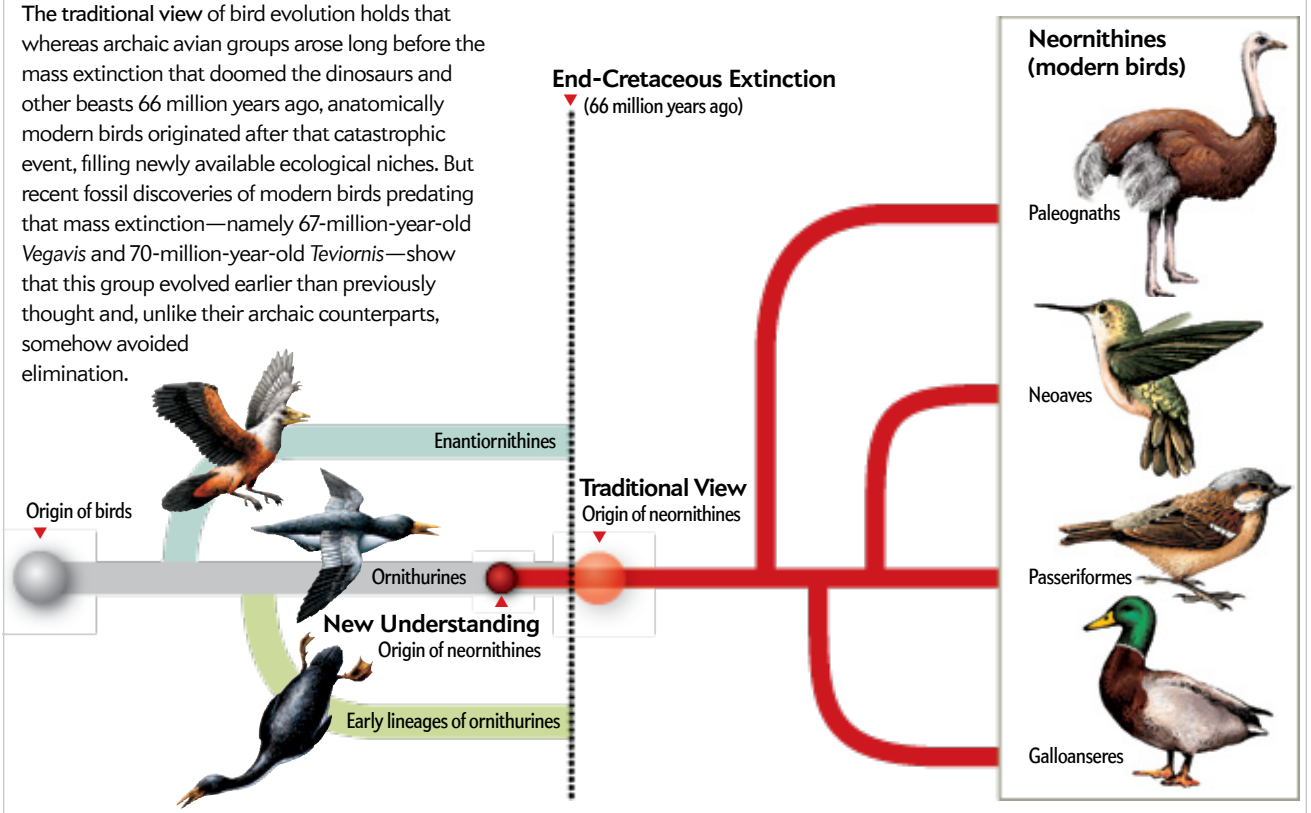
NEW FINDING

Earlier Origin

The traditional view of bird evolution holds that whereas archaic avian groups arose long before the mass extinction that doomed the dinosaurs and other beasts 66 million years ago, anatomically modern birds originated after that catastrophic event, filling newly available ecological niches. But recent fossil discoveries of modern birds predating that mass extinction—namely 67-million-year-old *Vegavis* and 70-million-year-old *Teviornis*—show that this group evolved earlier than previously thought and, unlike their archaic counterparts, somehow avoided elimination.



group). The DNA studies concluded that these two lineages—the most primitive of the living neornithines—split from each other deep in the Cretaceous. And researchers obtained similarly ancient divergence dates for other lineages.

The findings implied that, contrary to conventional paleontological wisdom, neornithines lived alongside dinosaurs. It is funny to think of a robin perched on the back of a *Velociraptor* or a duck paddling alongside a *Spinosaurus*. But the molecular evidence for the contemporaneity of modern birds and dinosaurs was so compelling that even the paleontologists—who have typically viewed with skepticism those DNA findings that conflict with the fossil record—began to embrace it. Still, those of us who study ancient skeletons urgently wanted fossil confirmation of this new view of bird evolution.

WHY WERE MODERN BIRDS ABLE TO SURVIVE THE ASTEROID IMPACT AND ITS ATTENDANT ECOLOGICAL CHANGES WHEN THEIR MORE PRIMITIVE AVIAN COUSINS AND THEIR FELLOW FLIERS, THE PTEROSAURS, WERE NOT?

DUCKS IN A ROW

AT LAST, after the new millennium, paleontologists' luck began to change for the better, starting with the tiny Mongolian wing that Evgeny and I focused on in Moscow. Back when Evgeny first saw the fossil in 1987, he told me that he thought it looked like a member of the presbyornithids, a group of now extinct ducklike birds related to modern ducks and geese. But at 70 million years old, it was a Cretaceous bird, and everyone knew—or thought they did—that there was no definitive evidence for presbyornithids in the Cretaceous. Yet our comparisons in the museum that cold winter in 2001 demonstrated conclusively that the wing—with its straight carpometacarpus (the bone formed by the fusion of the hand bones) and details of canals, ridges and muscle scars—did indeed belong to a presbyornithid, which, moreover, was the oldest unequivocal representative of any neornithine group. Our finding fit the predictions of the molecular biologists perfectly. In a 2002 paper that formally described the animal, we gave it the name *Teviornis*.

Before long, *Teviornis* was joined by a second confirmed early neornithine, *Vegavis,* from Antarctica's Vega Island. *Vegavis* had been found in the 1990s only to languish in relative anonymity for years before its true significance came to light. In 2005 Julia A. Clarke, now at the University of Texas at Austin, and her colleagues published a paper showing that *Vegavis* was another bird from the Cretaceous that exhibits a number of features found in modern ducks, particularly in its broad shoulder

SHAWN GOULD (*fossil birds* and *sparrow*); JEN CHRISTIANSEN (*ostrich, hummingbird* and *duck*)

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girdle, pelvis, wing bones and lower legs. At 68 million to 66 million years old, *Vegavis* is a little younger than *Teviornis* but still clearly predates the mass extinction. And it is a much more complete fossil, preserving the better part of a skeleton.

For most paleontologists, *Vegavis* clinched the case for Cretaceous neornithines. Thus enlightened, researchers have begun reexamining fossil collections from this time period, looking for additional examples of early modern birds. One investigator, Sylvia Hope of the California Academy of Sciences in San Francisco, had been arguing for years that bird species she has identified from fossils found in New Jersey and Wyoming that date to between 100 million and 80 million years ago are modern. But the finds—mostly single bones—had been considered by other researchers as too scrappy to identify conclusively. The revelations about *Vegavis* and *Teviornis* suggest that she was right all along. Comparisons of Hope's bones with more complete remains should prove illuminating in this regard.

FLYING THE COOP

ROOTING MODERN BIRDS in the Cretaceous neatly aligned the fossil record with the DNA-based divergence dates. But it raised a vexing new question: Why were modern birds able to survive the asteroid impact and its attendant ecological changes when their more primitive avian cousins and their fellow fliers, the pterosaurs, were not? To my mind, this constitutes the single biggest remaining mystery of bird evolution. The answer is still very much up for grabs, and I am devoting much of my research at the moment to trying to get at it.

With only a couple of confirmed Cretaceous neornithines on record, there is not much in the way of fossil clues to go on. Insights have come from studies of living birds, however. Using a huge data set of measurements of living birds, my colleagues in the U.K. and I have shown, for example, that the wing-bone proportions of primitive modern birds, including *Teviornis* and *Vegavis,* are no different from those of the extinct enantiornithines. Comparing the fossil wing-bone proportions with those of living birds allows us to infer some aspects of wing shape and hence gain information about the aerodynamic capabilities of fossil birds. But so far as we can tell, the wing shapes of the two groups of fossil birds do not differ; in other words, we do not think that early neornithines were any better at flying than were the enantiornithines (although both these groups were most likely better in the air than earlier theropodlike birds such as *Archaeopteryx*).

If flight ability did not give the neornithines an advantage over their Cretaceous counterparts, what did? A number of paleontologists, including me, have posited that differences in foraging habits might have conferred a competitive edge. In support of that theory, I have shown in a series of papers published over the past few years that modern birds preserved in the immediate aftermath of the mass extinction, in rocks 60 million years old and younger, probably lived mostly in wet environments: coastlines, lakes, the edges of rivers and the deep ocean, for example. Many of the birds that inhabit such environments today—ducks among them—are typically generalists, able to subsist on a wide variety of foods. And ducklike birds are currently the one confirmed lineage of modern birds we have found in the Cretaceous. The groups of Cretaceous birds that did not survive the disaster, in contrast, have been collected from rocks that were formed in many different kinds of environments—including seashores, inland areas, deserts and forests.

HARD EVIDENCE: Partial skeleton of *Vegavis* from Antarctica's Vega Island reveals a 67-million-year-old bird with distinctly modern features, including a broad shoulder girdle and fused wing bones.

This ecological diversity may indicate that the archaic birds had evolved specializations for feeding in each of these niches. Perhaps, then, the secret of early modern birds' success was simply the fact that they were less specialized than the other groups.

Such flexibility might have enabled the neornithines to adapt more easily to the changing conditions that followed the asteroid impact. It is an appealing idea, but these are early days. Only with the discovery of more fossils—whether in the ground or in museum drawers—will we be able to determine how modern birds eluded elimination and took wing. SA

Gareth Dyke is a paleontologist at the University of Southampton in England, where he studies the evolutionary history of dinosaurs and birds. He is writing a novel inspired by the life of Baron Franz Nopcsa, who discovered and described some of the first dinosaurs from Central Europe.

MORE TO EXPLORE

A New Presbyornithid Bird (Aves, Anseriformes) from the Late Cretaceous of Southern Mongolia. E. N. Kurochkin, G. J. Dyke and A. A. Karhu in *American Museum Novitates,* No. 3866, pages 1–12; December 27, 2002.

Definitive Fossil Evidence for the Extant Avian Radiation in the Cretaceous. Julia A. Clarke et al. in *Nature,* Vol. 433, pages 305–308; January 20, 2005.

The Beginnings of Birds: Recent Discoveries, Ongoing Arguments and New Directions. Luis M. Chiappe and Gareth J. Dyke in *Major Transitions in Vertebrate Evolution.* Edited by J. S. Anderson and H.-D. Sues. Indiana University Press, 2007.

The Inner Bird: Anatomy and Evolution. Gary W. Kaiser. University of British Columbia Press, 2007.

Living Dinosaurs: The Evolutionary History of Modern Birds. Edited by Gareth Dyke and Gary Kaiser. John Wiley & Sons, 2011.

scientificamerican.com/magazine/sa

FROM "DEFINITIVE FOSSIL EVIDENCE FOR THE EXTANT AVIAN RADIATION IN THE CRETACEOUS" BY JULIA A. CLARKE ET AL., IN *NATURE,* VOL. 433; JANUARY 20, 2005

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ANATOMY

WHICH CAME FIRST, THE FEATHER OR THE BIRD?

A long-cherished view of how and why feathers evolved has now been overturned

By Richard O. Prum and Alan H. Brush

Illustration by Kazuhiko Sano

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FEATHERS EVOLVED in carnivorous, bipedal dinosaurs before the origin of birds. The creatures depicted here are reconstructions of fossils found in northern China that show clear traces of feathers. The large dinosaur eating a lizard is *Sinornithosaurus;* to its right is *Sinosauropteryx;* and the small dinosaur on the tree limb is *Microraptor.*

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HAIR, SCALES, FUR, FEATHERS. OF ALL THE BODY COVERINGS NATURE has designed, feathers are the most various and the most mysterious. How did these incredibly strong, wonderfully lightweight, amazingly intricate appendages evolve? Where did they come from? Only in around the past two decades have we begun to answer this question. Several lines of research have converged on a remarkable conclusion: the feather evolved in dinosaurs before the appearance of birds.

The origin of feathers is a specific instance of the much more general question of the origin of evolutionary novelties—structures that have no clear antecedents in ancestral animals and no clear related structures (homologues) in contemporary relatives. Although evolutionary theory provides a robust explanation for the appearance of minor variations in the size and shape of creatures and their component parts, it does not yet give as much guidance for understanding the emergence of entirely new structures, including digits, limbs, eyes and feathers.

Progress in solving the particularly puzzling origin of feathers has also been hampered by what now appear to be false leads, such as the assumption that the primitive feather evolved by elongation and division of the reptilian scale, and speculations that feathers evolved for a specific function, such as flight. A lack of primitive fossil feathers hindered progress as well. For many years the earliest bird fossil has been *Archaeopteryx lithographica,* which lived in the Late Jurassic period (about 148 million years ago). But *Archaeopteryx* offers no new insights on how feathers evolved, because its own feathers are nearly indistinguishable from those of today's birds.

Contributions from several fields have put these traditional problems to rest. First, biologists have begun to find fresh evidence for the idea that developmental processes—the complex mechanisms by which an individual organism grows to its full size and form—can be a window into the evolution of a species' anatomy. This idea has been reborn as the field of evolutionary developmental biology, or "evo-devo." It has given us a powerful tool for probing the origin of feathers. Second, paleontologists have unearthed a trove of feathered dinosaurs in China. These animals have a diversity of primitive feathers that are not as highly evolved as those of today's birds or even *Archaeopteryx*. They are critical clues to the structure, function and evolution of modern birds' intricate appendages.

Together these advances have produced an extremely detailed and revolutionary picture: feathers originated and diversified in carnivorous, bipedal theropod dinosaurs before the origin of birds or the origin of flight.

THE TOTALLY TUBULAR FEATHER

THIS SURPRISING PICTURE was pieced together thanks in large measure to a new appreciation of exactly what a feather is and how it develops in modern birds. Like hair, nails and scales, feathers are integumentary appendages—skin organs that form by controlled proliferation of cells in the epidermis, or outer skin layer, that produce the keratin proteins. A typical feather features a main shaft, called the rachis [*see box on opposite page*]. Fused to the rachis are a series of branches, or barbs. In a fractal-like reflection of the branched rachis and barbs, the barbs themselves are also branched: a series of paired filaments called barbules are fused to the main shaft of the barb, the ramus. At the base of the feather, the rachis expands to form the hollow tubular calamus, or quill, which inserts into a follicle in the skin. A bird's feathers are replaced periodically during its life through molt—the growth of new feathers from the same follicles.

Variations in the shape and microscopic structure of the barbs,

IN BRIEF

Dinosaur fossils found in China have feathers that are more primitive than those of modern birds or even of the oldest known bird fossil.

The Chinese fossils provide evidence that feathers originated and diversified in bipedal, carnivorous dinosaurs before the origin of birds or flight. Variations in shape and microscopic structure determine the functions of different types of feathers, such as flight and insulation.

Feathers probably evolved in stages, beginning with a simple tubular feather, with each stage evolving in a particular group of dinosaurs.

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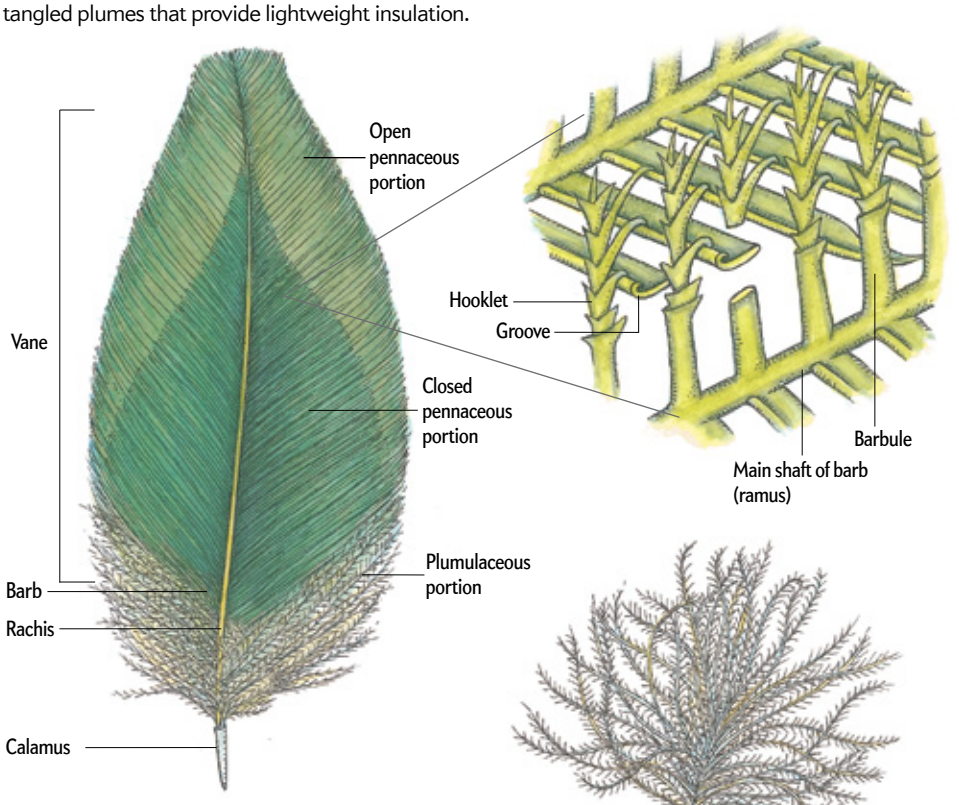
VARIATIONS

The Nature of Feathers

Feathers display an amazing diversity and serve almost as wide a range of functions, from courtship to camouflage to flight. Variations in the shapes of a feather's components—the barbs, barbules and rachis—create this diversity. Most feathers, however, fall into two basic types. The pennaceous is the iconic feather of a quill pen or a bird's wing. The plumulaceous, or downy, feather has soft, tangled plumes that provide lightweight insulation.



Pennaceous Feather

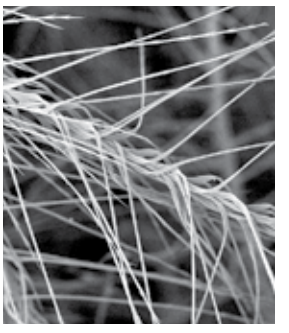
Paired barbs fused to the central rachis create the defining vane of a pennaceous feather. In the closed pennaceous portion of the vane, tiny hooklets on one barbule interlock with grooves in the neighboring barbule (*detail* and *middle micrograph*) to form a tight, coherent surface. In the open pennaceous portion, the barbules do not hook together. Closed pennaceous feathers are essential for avian flight.

Plumulaceous (Downy) Feather

A plumulaceous feather has no vane. It is characterized by a rudimentary rachis and a jumbled tuft of barbs with elongated barbules.

Open pennaceous vane

Closed pennaceous vane



Plumulaceous (downy) feather

Downy Feather

Fluffy structure provides insulation.

Contour Feather

Planar vane helps to form the outline of the body.

Flight Feather

Asymmetrical vane creates aerodynamic forces.

Pinfeathers

Newly emerged, incompletely developed feathers are visible on these toucan chicks.

TIM LEE QUINN (*feather micrographs*); TINA WEST (*feather photographs*); ZSSD *Corbis (baby toucans)*

Illustrations by Patricia J. Wynne

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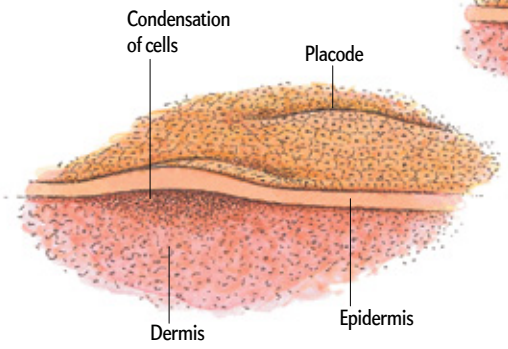
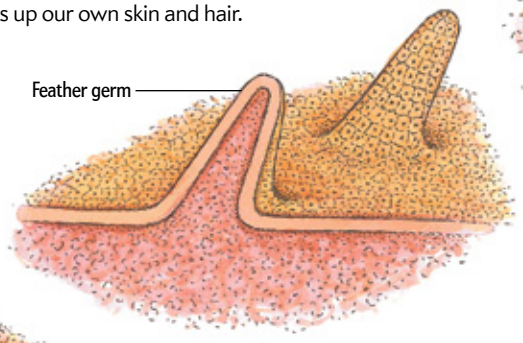
STAGES

How Feathers Grow

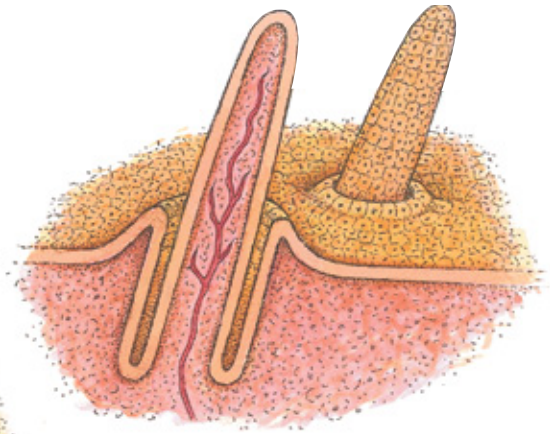
As in hair, nails and scales, feathers grow by proliferation and differentiation of keratinocytes. These keratin-producing cells in the epidermis, or outer skin layer, achieve their purpose in life when they die, leaving behind a mass of deposited keratin. Keratins are filaments of proteins that polymerize to form solid structures. Feathers are made of beta-keratins, which are unique to reptiles and birds. The outer covering of the growing feather, called the sheath, is made of the softer alpha-keratin, which is found in all vertebrates and makes up our own skin and hair.



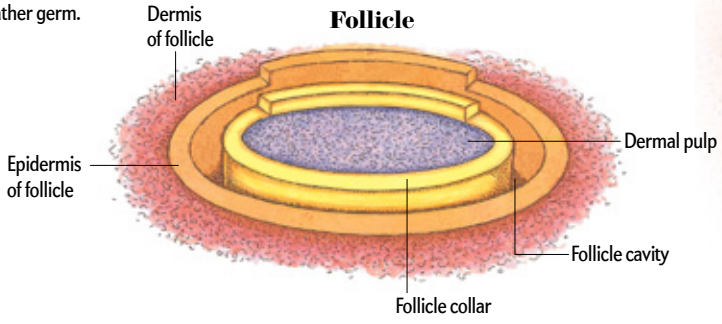
Feather growth begins with the placode, a thickening of the epidermis over a condensation of cells in the dermis.



The placode then forms a unique elongated tube, the feather germ.



Proliferation of cells in a ring around the feather germ creates the follicle (*detail below*), the organ that generates the feather. At the base of the follicle, in the follicle collar, the continuing production of keratinoctyes forces older cells up and out, eventually forming the entire, tubular feather.



barbules and rachis create an astounding range of feathers. But despite this diversity, most feathers fall into two structural classes. A typical pennaceous feather has a prominent rachis and barbs that create a planar vane. The barbs in the vane are locked together by pairs of specialized barbules. The barbules that extend toward the tip of the feather have a series of tiny hooklets that interlock with grooves in the neighboring barbules. Pennaceous feathers cover the bodies of birds, and their tightly closed vanes create the aerodynamic surfaces of the wings and tail. In dramatic contrast to pennaceous feathers, a plumulaceous, or downy, feather has only a rudimentary rachis and a jumbled tuft of barbs with long barbules. The long, tangled barbules give these feathers their marvelous properties of lightweight thermal insulation and comfortable loft. Feathers can have a pennaceous vane and a plumulaceous base.

In essence, all feathers are variations on a tube produced by proliferating epidermis with the nourishing dermal pulp in the center. And even though a feather is branched like a tree, it grows from its base like a hair. How do feathers accomplish this?

Feather growth begins with a thickening of the epidermis called the placode, which elongates into a tube—the feather germ [*see box above*]. Proliferation of cells in a ring around the feather germ creates a cylindrical depression, the follicle, at its base. The growth of keratin cells, or keratinocytes, in the epidermis of the follicle—the follicle "collar"—forces older cells up and out, eventually generating the entire feather in an elaborate choreography that is one of the wonders of nature.

As part of that choreography, the follicle collar divides into a series of longitudinal ridges—barb ridges—that create the separate barbs. In a pennaceous feather, the barbs grow helically around the tubular feather germ and fuse on one side to form the rachis. Simultaneously, new barb ridges form on the other side of the tube. In a plumulaceous feather, barb ridges grow straight without any helical movement. In both types of feather, the barbules that extend from the barb ramus grow from a single layer of cells, called the barbule plate, on the periphery of the barb ridge.

EVO-DEVO COMES TO THE FEATHER

TOGETHER WITH VARIOUS COLLEAGUES, we think the process of feather development can be mined to reveal the probable nature of the primitive structures that were the evolutionary precursors of feathers. Our developmental theory proposes that feathers evolved through a series of transitional stages, each marked by a developmental evolutionary novelty, a new mechanism of growth. Advances at one stage provided the basis for the next innovation [*see box on pages 82 and 83*].

In 1999 we proposed the following evolutionary scheme. Stage 1 was the tubular elongation of the placode from a feather germ and follicle. This yielded the first feather—an unbranched, hollow cylin-

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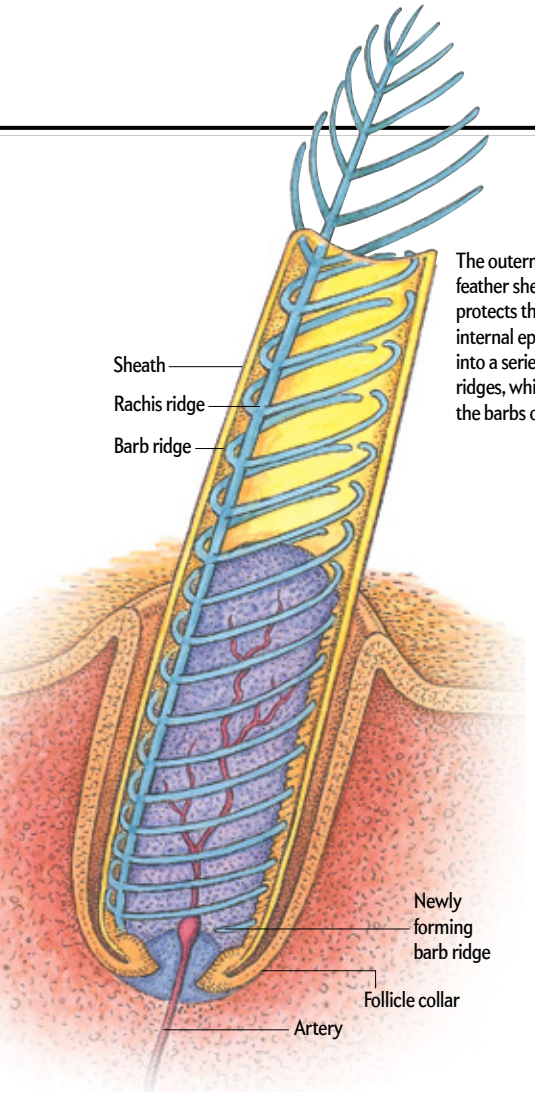
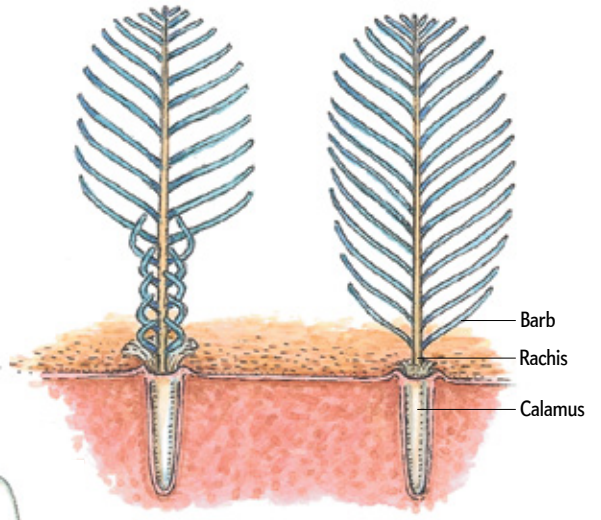
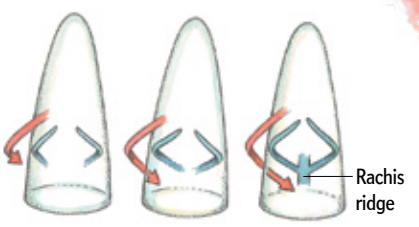


The outermost epidermal layer becomes the feather sheath, a temporary structure that protects the growing feather. Meanwhile the internal epidermal layer becomes partitioned into a series of compartments, called barb ridges, which subsequently grow to become the barbs of the feather.



As growth proceeds, the feather emerges from its superficial sheath. The feather then unfurls to obtain its planar shape. When the feather reaches its final size, the follicle collar forms the calamus, a simple tube at the base of the feather.

Helical Growth



In a pennaceous feather, the barb ridges grow helically around the collar until they fuse to form the rachis ridge. Subsequent barb ridges fuse to the rachis ridge. In a plumulaceous feather (*not shown*), barb ridges do not grow helically, and a simple rachis forms at the base of the feather.

der. Then, in stage 2, the follicle collar, a ring of epidermal tissue, differentiated (specialized): the inner layer became the longitudinal barb ridges, and the outer layer became a protective sheath. This stage produced a tuft of barbs fused to the hollow cylinder, or calamus.

The model has two alternatives for the next stage—either the origin of helical growth of barb ridges and formation of the rachis (stage 3a) or the origin of the barbules (3b). The ambiguity about which came first arises because feather development does not indicate clearly which event occurred before the other. A stage 3a follicle would produce a feather with a rachis and a series of simple barbs. A stage 3b follicle would generate a tuft of barbs with branched barbules. Regardless of which stage came first, the evolution of both these features, stage 3a+b, would yield the first double-branched feathers, exhibiting a rachis, barbs and barbules. Because barbules were still undifferentiated at this stage, a feather would be open pennaceous—that is, its vane would not form a tight, coherent surface in which the barbules are locked together.

In stage 4 the capacity to grow differentiated barbules evolved. This advance enabled a stage 4 follicle to produce hooklets at the ends of barbules that could attach to the grooved barbules of the adjacent barbs and create a pennaceous feather with a closed vane. Only after stage 4 could additional feather variations evolve, including the many specializations seen at stage 5, such as the asymmetrical vane of a flight feather.

THE SUPPORTING CAST

INSPIRATION FOR THE THEORY came from the hierarchical nature of feather development itself. The model hypothesizes, for example, that a simple tubular feather preceded the evolution of barbs because barbs are created by the differentiation of the tube into barb ridges. Likewise, a plumulaceous tuft of barbs evolved before the pennaceous feather with a rachis because the rachis is formed by the fusion of barb ridges. Similar logic underlies each of the hypothesized stages of the developmental model.

Support for the theory comes in part from the diversity of feathers among modern birds, which sport feathers representing every stage of the model. Obviously, these feathers are recent, evolutionarily derived simplifications that merely revert back to the stages that arise during evolution because complex feather diversity (through stage 5) must have evolved before *Archaeopteryx*. These modern feathers demonstrate that all the hypothesized stages are within the developmental capacity of feather follicles. Thus, the developmental theory of feather evolution does not require any purely theoretical structures to explain the origin of all feather diversity.

Support also comes from exciting molecular findings that have confirmed the first three stages of the evo-devo model. Technological advances allow us to peer inside cells and identify whether specific genes are expressed (turned on so that they can give rise to the

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products they encode). Several laboratories have combined these methods with experimental techniques that investigate the functions of the proteins made when their genes are expressed during feather development. Matthew Harris, now at Harvard Medical School, John F. Fallon of the University of Wisconsin–Madison and one of us (Prum) have studied two important pattern formation genes—*sonic hedgehog* (*Shh*) and *bone morphogenetic protein 2* (*Bmp2*). These genes play a crucial role in the growth of vertebrate limbs, digits, and integumentary appendages such as hair, teeth and nails. We found that Shh and Bmp2 proteins work as a modular pair of signaling molecules that, like a general-purpose electronic component, is reused repeatedly throughout feather development. The Shh protein induces cell proliferation, and the Bmp2 protein regulates the extent of proliferation and fosters cell differentiation.

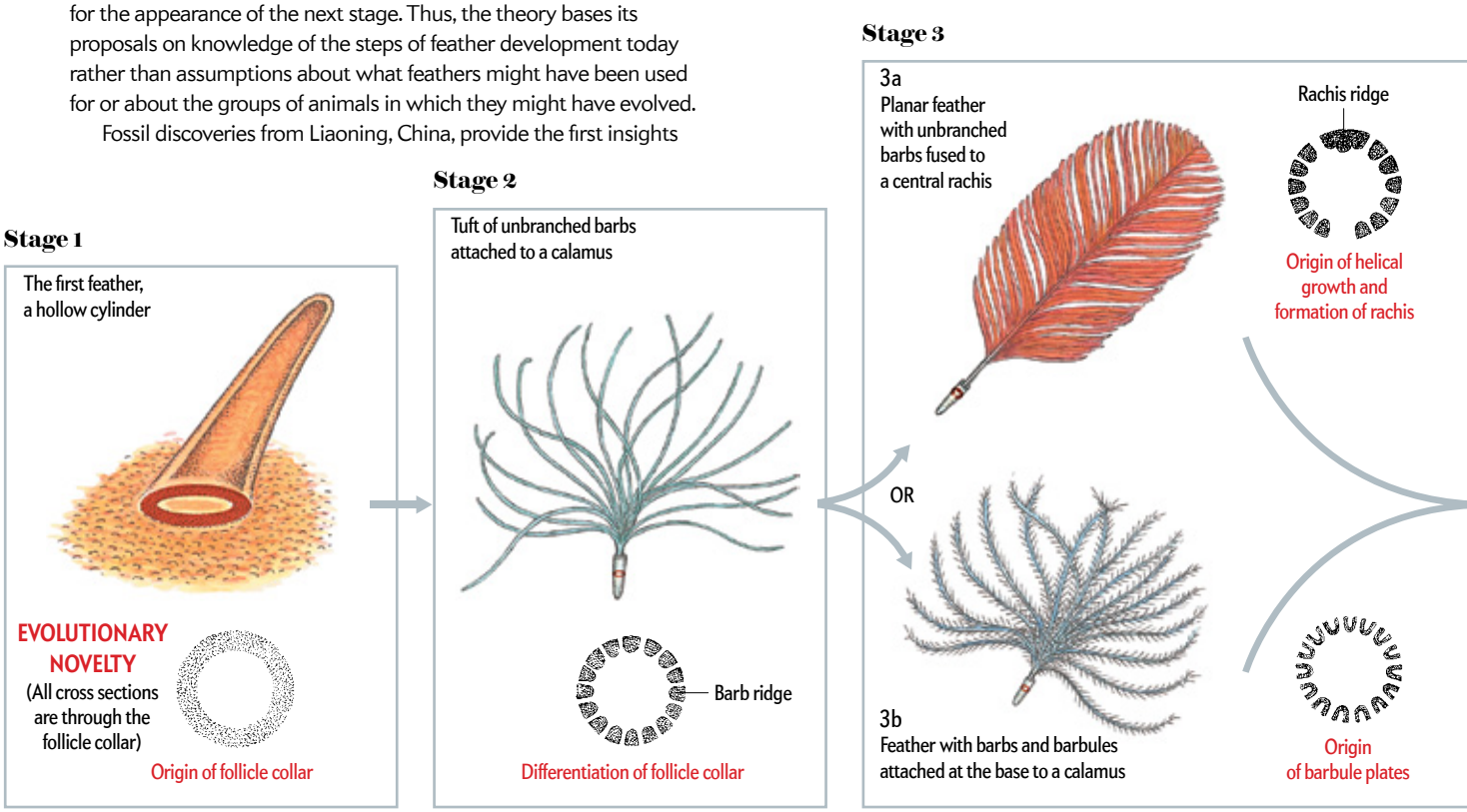
The expression of Shh and Bmp2 begins in the feather placode, where the pair of proteins is produced in a polarized anterior-posterior pattern. Next, Shh and Bmp2 are both expressed at the tip of the tubular feather germ during its initial elongation and, fol-

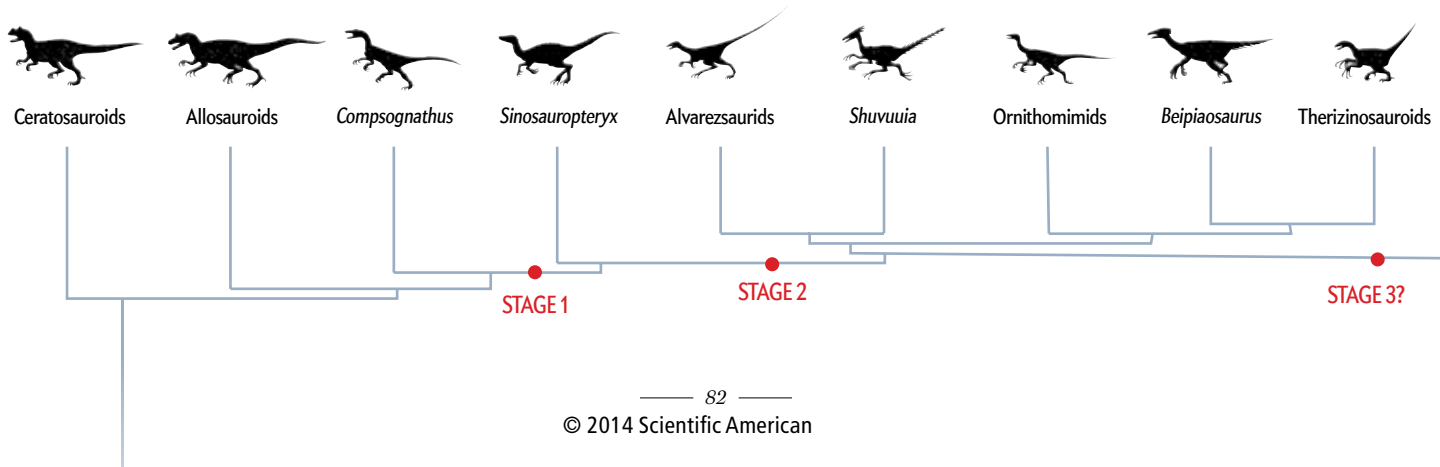
FINDINGS

Evo-Devo and the Feather

The authors' theory of feather origin grew out of the realization that the mechanisms of development can help explain the evolution of novel features—a field dubbed evo-devo. The model proposes that the unique characteristics of feathers evolved through a series of evolutionary novelties in how they grow, each of which was essential for the appearance of the next stage. Thus, the theory bases its proposals on knowledge of the steps of feather development today rather than assumptions about what feathers might have been used for or about the groups of animals in which they might have evolved.

Fossil discoveries from Liaoning, China, provide the first insights into which theropod dinosaurs evolved the feathers of each hypothesized stage. Based on the similarities between the primitive feather predictions of the model and the shapes of the fossil skin appendages, the authors suggest that each stage evolved in a particular group of dinosaurs.


Stage 1
The first feather, a hollow cylinder
EVOLUTIONARY NOVELTY
(All cross sections are through the follicle collar)
Origin of follicle collar
Stage 2
Tuft of unbranched barbs attached to a calamus
Barb ridge
Differentiation of follicle collar
Stage 3
3a
Planar feather with unbranched barbs fused to a central rachis
Rachis ridge
Origin of helical growth and formation of rachis
OR
3b
Feather with barbs and barbules attached at the base to a calamus
Origin of barbule plates



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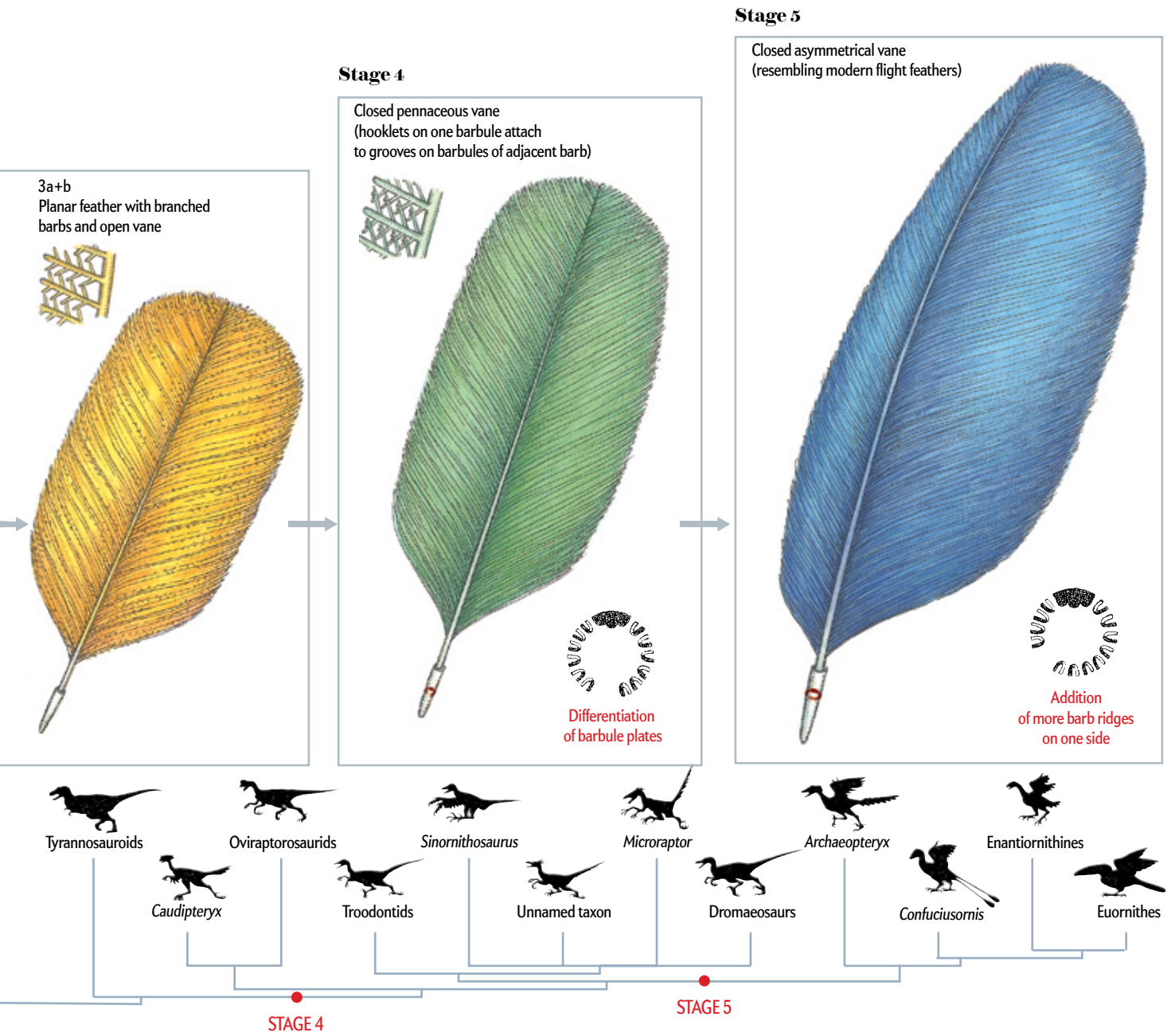
lowing that, in the epithelium that separates the forming barb ridges, establishing a pattern for the growth of the ridges. Then, in pennaceous feathers, the Shh and Bmp2 signaling lays down a pattern for helical growth of barb ridges and rachis formation, whereas in plumulaceous feathers the Shh and Bmp2 signals create a simpler pattern of barb growth. Each stage in the development of a feather has a distinct pattern of Shh and Bmp2 signaling. Again and again the two proteins perform critical tasks as the feather unfolds to its final form.

These molecular data confirm that feather development is composed of a series of hierarchical stages in which subsequent events are mechanistically dependent on earlier stages. For example, the evolution of longitudinal stripes in Shh-Bmp2 expression is contingent on the prior development of an elongate tubular feather germ. Likewise, the variations in Shh-Bmp2 patterning during pennaceous feather growth are contingent on the prior establishment of the longitudinal stripes. Thus, the molecular data are beautifully consistent with the scenario that feathers evolved from an elon-



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SPECIMEN of *Microraptor gui* (*above*) shows asymmetrical feathers, blurring the distinction between birds and dinosaurs. Fossils found in quarries in Liaoning Province, China, such as this *Caudipteryx* forelimb (*left*), reveal feathered appendages. This dinosaur, which was roughly the size of a turkey, has excellently preserved pennaceous feathers on its tail as well as its forelimbs.

gate hollow tube (stage 1), to a downy tuft of barbs (stage 2), to a pennaceous structure (stage 3a).

THE STARS OF THE DRAMA

CONCEPTUAL THEORIES have spurred our thinking, and state-of-the-art laboratory techniques have enabled us to eavesdrop on the cell as it gives life and shape to a feather. But plain old-fashioned detective work in fossil-rich quarries in northern China has turned up the most spectacular evidence for the developmental theory. Chinese, American and Canadian paleontologists in Liaoning Province have unearthed a startling trove of fossils in the Early Cretaceous Yixian Formation (128 million to 124 million years old). Excellent conditions in the formation have preserved an array of ancient organisms, including the earliest placental mammal, the earliest flowering plant, an explosion of ancient birds and a diversity of theropod dinosaur fossils with sharp integumentary details. Various dinosaur fossils clearly show fully modern feathers and a diversity of primitive feather structures. The conclusions are inescapable: feathers originated and evolved their essentially modern structure in a lineage of terrestrial, bipedal, carnivorous dinosaurs before the appearance of birds or flight.

The first feathered dinosaur found there, in 1997, was a chicken-sized coelurosaur (*Sinosauropteryx*); it had small tubular and perhaps branched structures emerging from its skin. Next the paleontologists discovered a turkey-sized oviraptoran dinosaur (*Caudipteryx*) that had beautifully preserved, modern-looking pennaceous feathers on the tip of its tail and forelimbs. Some skeptics have claimed that *Caudipteryx* was merely an early flightless bird, but many phylogenetic analyses place it among the oviraptoran theropod dinosaurs. Subsequent discoveries at Liaoning have revealed pennaceous feathers on specimens of dromaeosaurs, the theropods that are hypothesized to be most closely related to birds but that clearly are not birds. In all, investigators found fossil feathers from more than a dozen nonavian theropod dinosaurs, among them the ostrich-sized therizinosaur *Beipiaosaurus* and a variety of dromaeosaurs, including *Microraptor* and *Sinornithosaurus*.

The heterogeneity of the feathers found on these dinosaurs is striking and provides strong direct support for the developmental theory. The most primitive feathers known—those of *Sinosauropteryx*—are the simplest tubular structures and are remarkably like the predicted stage 1 of the developmental model. *Sinosauropteryx, Sinornithosaurus* and some other nonavian theropod specimens show open tufted structures that lack a rachis and are strikingly congruent with stage 2 of the model. There are also pennaceous feathers that obviously had differentiated barbules and coherent planar vanes, as in stage 4 of the model.

These fossils open a new chapter in the history of vertebrate skin. We now know that feathers first appeared in a group of theropod dinosaurs and diversified into essentially modern structural variety within other lineages of theropods before the origin of birds. Among the numerous feather-bearing dinosaurs, birds represent one particular group that evolved the ability to fly using the feathers of its specialized forelimbs and tail. *Caudipteryx, Protopteryx* and dromaeosaurs display a prominent "fan" of feathers at the tip of the tail, indicating that even some aspects of the plumage of modern birds evolved in theropods.

MICK ELLISON *American Museum of Natural History (left);* XING XU *(right)*

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The consequence of these amazing fossil finds has been a simultaneous redefinition of what it means to be a bird and a reconsideration of the biology and life history of the theropod dinosaurs. Birds—modern birds and the group that includes all species descended from the most recent common ancestor of *Archaeopteryx*—used to be recognized as the flying, feathered vertebrates. Now we must acknowledge that birds are a group of the feathered theropod dinosaurs that evolved the capacity of powered flight. New fossil discoveries have continued to close the gap between birds and dinosaurs and ultimately make it more difficult even to define birds. Conversely, many of the most charismatic and culturally iconic dinosaurs, such as *Tyrannosaurus* and *Velociraptor,* are very likely to have had feathered skin but were not birds.

DINOSAUR OR BIRD? THE GAP NARROWS

THE DISTINCTIONS between birds and dinosaurs continue to diminish with every new discovery. In 2003 Xing Xu and Zhonghe Zhou of the Institute of Vertebrate Paleontology and Paleoanthropology at the Chinese Academy of Sciences described some remarkable new specimens of *Microraptor gui,* a dromaeosaur in the group of theropods that are most closely related to birds. The creatures have asymmetrical feathers on both their arms and legs. In living birds, feathers with asymmetrical vanes function in flight. *Microraptor* had four wings—two on its arms and two on its legs—that apparently had an aerodynamic function. Xu and his colleagues hypothesize that *Microraptor* was an advanced glider, and because *Microraptor* is in the group that is most closely related to birds, they further propose that the two-winged powered flight of birds evolved through a similar four-winged gliding ancestor.

The debate on the origin of bird flight has focused on two competing hypotheses: flight evolved from the trees through a gliding stage, or flight evolved from the ground through a powered running stage. The trees-down theory gets some support from the discovery of a functional glider in the theropod dinosaurs most closely related to birds. Many questions remain, of course, including how *Microraptor* actually used its four wings.

For thousands of years, humans have believed that feathers and feather-powered flight were unique to birds. But we have learned that feathers evolved and diversified in theropod dinosaurs before the origin of birds and discovered that even some aspects of avian flight may not be unique to birds. Both of the historical claims to the status of the birds as a special class of vertebrates—feathers and flight—have evaporated. Although this realization may disappoint some people, the disappearance of large gaps in our knowledge about the tree of life represents a great success for evolutionary biology.

A FRESH LOOK

THANKS TO THE DIVIDENDS provided by relatively recent findings, researchers can now reassess the various earlier hypotheses about the origin of feathers. The new evidence from developmental biology is particularly damaging to the classical theory that feathers evolved from elongate scales. According to this scenario, scales evolved into feathers by first elongating, then growing fringed edges, and finally producing hooked and grooved barbules. As we have seen, however, feathers are tubes; the two planar sides of the vane—the front and the back—are created by the inside and outside of the tube only after the feather unfolds from its cylindrical sheath. In contrast, the two planar sides of a scale develop from the top and bottom of the initial epidermal outgrowth that forms the scale.

The fresh evidence also puts to rest the popular and enduring theory that feathers evolved primarily or originally for flight. Only highly evolved feather shapes—namely the asymmetrical feather with a closed vane, which did not occur until stage 5—could have been used for flight. Proposing that feathers evolved for flight now appears to be like hypothesizing that fingers evolved to play the piano. Rather feathers were "exapted" for their aerodynamic function only after the evolution of substantial developmental and structural complexity. They evolved for some other purpose and were then exploited for a different use.

Numerous other proposed early functions of feathers remain plausible, including insulation, water repellency, courtship, camouflage and defense. Even with the wealth of new paleontological data, though, it seems unlikely that we will ever gain sufficient insight into the biology and natural history of the specific lineage in which feathers evolved to distinguish among these hypotheses. Instead our theory underscores that feathers evolved by a series of developmental innovations, each of which may have evolved for a different original function. We do know, however, that feathers emerged only after a tubular feather germ and follicle formed in the skin of some species. Hence, the first feather evolved because the first tubular appendage that grew out of the skin provided some kind of survival advantage.

Creationists and other evolutionary skeptics have long pointed to feathers as a favorite example of the insufficiency of evolutionary theory. There were no transitional forms between scales and feathers, they have argued. Further, they asked why natural selection for flight would first divide an elongate scale and then evolve an elaborate new mechanism to weave it back together. Now, in an ironic about-face, feathers offer a sterling example of how we can best study the origin of an evolutionary novelty: focus on understanding those features that are truly new and examine how they form during development in modern organisms. This new paradigm in evolutionary biology is certain to penetrate many more mysteries. Let our minds take wing. SA

Richard O. Prum and **Alan H. Brush** share a passion for feather biology. Prum, who started bird-watching at the age of 10, is now William Robertson Coe Professor of Ornithology in the department of ecology and evolutionary biology at Yale University. He also serves as curator of ornithology and head curator of vertebrate zoology at the Peabody Museum of Natural History there. His research has focused on avian phylogeny, avian courtship and breeding systems, the physics of structural colors and the evolution of feathers. He has conducted field studies in Central and South America, Madagascar and New Guinea. Brush is emeritus professor of physiology and neurobiology at the University of Connecticut. He has worked on feather pigment and keratin biochemistry and the evolution of feather novelties. He was editor of *The Auk*.

MORE TO EXPLORE

Development and Evolutionary Origin of Feathers. Richard O. Prum in *Journal of Experimental Zoology (Molecular and Developmental Evolution),* Vol. 285, No. 4, pages 291–306; December 15, 1999.

Evolving a Protofeather and Feather Diversity. Alan H. Brush in *American Zoologist,* Vol. 40, No. 4, pages 631–639; 2000.

***Shh-Bmp2* Signaling Module and the Evolutionary Origin and Diversification of Feathers.** Matthew P. Harris, John F. Fallon and Richard O. Prum in *Journal of Experimental Zoology,* Vol. 294, No. 2, pages 160–176; August 15, 2002.

The Evolutionary Origin and Diversification of Feathers. Richard O. Prum and Alan H. Brush in *Quarterly Review of Biology,* Vol. 77, No. 3, pages 261–295; September 2002.

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PROFILE

THE DINOSAUR BARON OF TRANSYLVANIA

A maverick aristocrat's ideas about dinosaur evolution turn out to have been decades ahead of their time

By Gareth Dyke

THE YEAR IS 1906. A SMALL, NATTILY DRESSED MAN walks over to the giant *Diplodocus* skeleton in the entrance hall of the British Museum of Natural History. He gently lifts one of the dinosaur's huge toe bones out of its iron mount, flips it over and carefully slips it back into place. Later he would note in correspondence to a colleague that his effort was not appreciated. The museum officials should have known better. The visitor was Franz Nopcsa (pronounced "nop-cha"), baron of Szacsal in Transylvania. In addition to being a nobleman, he was an esteemed authority on dinosaurs and other fossil animals. The baron had noticed that the *Diplodocus* toe bone was oriented incorrectly and was simply trying to fix it. Although Nopcsa failed to garner the respect of the officials, history has been somewhat kinder to him. Among paleontologists today, he is well known for having discovered and described some of the first dinosaurs from central Europe. Yet the details of Nopcsa's personal life have often overshadowed his intellectual legacy. Adventurous, eccentric and wildly ambitious, Nopcsa was a colorful character. He served as a spy in World War I and made a bid to become king of Albania. He was also openly homosexual; his lover and secretary was a much younger Albanian man named Bajazid Elmaz Doda.

But there was much more to Nopcsa than his fossil collection and his personal and political affairs, as recent findings have underscored. He pioneered techniques for fossil analysis that are still at the forefront of paleontological research. Moreover, his theories about dinosaur evolution turn out to have been decades ahead of their time. Nopcsa insisted that his Transylvanian dinosaurs were key to understanding dinosaur evolution on a global scale. Only in recent years, with new fossil discoveries, have scientists begun to appreciate how right he was.

ISLAND OF DWARFS

NOPCSA FIRST ENCOUNTERED FOSSILS in 1895, when his sister, Ilona, happened on some large bones on one of the family estates in Transylvania, then part of Austria-Hungary. He pounced on the remains and brought some to Vienna, where he was attending secondary school, to show to a geology professor. The professor informed him they were from dinosaurs and offered him the assistance of one of the department technicians to collect more remains and to prepare a formal description. But although he

Illustration by Jack Unruh

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had hardly any training in paleontology, the 18-year-old Nopcsa decided to go it alone, working day and night to learn anatomy. He was quick: within a year he wrote a paper on Ilona's bones describing a new species of ornithopod dinosaur from Transylvania, later dubbed *Telmatosaurus*.

It was the beginning of a long and productive career for Nopcsa: over the next 35 years he published more than 100 scientific papers on fossils, many of them cutting-edge. He was one of the first to investigate whether the anatomy of long-extinct animals and how they had been fossilized together could be used to understand how they interacted in life; he championed the Victorian notion that birds were a kind of dinosaur, rather than the distant reptilian relatives his colleagues believed them to be—a view that has since gained acceptance by the vast majority of modern paleontologists; he charted the geology of enormous swaths of Central Europe; and the list goes on and on.

Nopcsa traveled far and wide in his scientific pursuits, but his most important work derived from discoveries made in his own backyard. The baron noticed, for example, that *Telmatosaurus,* the dwarf sauropod *Magyarosaurus* (a genus name coined by German paleontologist Friedrich von Huene to replace Nopcsa's use of *Titanosaurus*) and other dinosaurs found on the Nopcsa estates were significantly smaller than other closely related species. *Magyarosaurus,* for one, was just six meters long—tiny compared with other sauropods, which routinely reached lengths of 15 to 20 meters. Because Nopcsa was an accomplished geologist, he knew that back when *Magyarosaurus* roamed Transylvania some 70 million years ago, at the end of the Cretaceous period, a warm, shallow sea called Tethys covered much of Southern Europe, leaving only islands of elevated regions suitable for terrestrial creatures. He also knew that some island-dwelling mammals, such as the recently extinct Mediterranean elephants, had evolved small bodies, presumably an adaptation to the limited resources available in these environments. Putting two and two together, he proposed in 1914 that the burial ground of his dinosaurs had once been part of an island born of the flooding of Europe by the Tethys Sea. He called this putative island Hátszeg and argued that his dinosaurs had attained their pint-size proportions as a result of island dwarfing.

Although Nopcsa's contemporaries would have known about the pony-size elephants from Crete and other Mediterranean islands, no one had ever proposed that such shrinking could occur in dinosaurs. The baron's bold theory was largely ignored. But starting in the late 1970s, renewed interest in the Late Cretaceous beasts of Transylvania put Nopcsa's dwarfing scenario back on the table. Since then, it has gained considerable support, in part because discoveries of other dinosaurs have confirmed that the Hátszeg dinosaurs were significantly smaller than their counterparts elsewhere in Europe, as well as those in Asia and North America.

Recently my own work has bolstered Nopcsa's ideas. In studying a collection of Early Cretaceous bones unearthed from a Transylvanian bauxite mine in the 1970s, I discovered a number of very small birds and pterosaurs represented among the remains. Judging from preserved wing elements, I surmised that the creatures were probably capable of flying long distances. As I reported in 2010 in a paper published in *Palaeontology,* these are exactly the kinds of flying animals one would expect to find on an isolated island. In fact, the species preserved in the bauxite mine collection are similar to the ones Nopcsa found in Hátszeg, a few hundred kilometers to the east. The bauxite mine locality was part of another earlier island in the Cretaceous archipelago formed by the Tethys.

Fittingly, evidence obtained using a technique Nopcsa himself invented has provided some of the strongest support for his island-dwarfing theory. In the 1930s Nopcsa published a revolutionary paper in which he described having exploited the microscopic structure, or histology, of bone to show that a fossil of an allegedly new type of duck-billed dinosaur from North America was actually just a juvenile member of a previously known species. He had figured out that he could estimate how old an animal was when it died based on the histology visible in thin slices of bone when viewed under high magnification, much as one can count growth rings to determine the age of a tree.

One of the weak spots in Nopcsa's dwarf dinosaur theory, when he first proposed it, was that he could not exclude the possibility that his dinos were small simply because they were juveniles. He passed away before he could apply his histology technique to the problem. But recently a group of German, American and Romanian paleontologists conducted histological studies on *Magyarosaurus* and concluded that the dainty sauropod was indeed fully grown, upholding Nopcsa's interpretation of the remains as those of an island dwarf. The team published its findings in 2010 in the *Proceedings of the National Academy of Sciences USA*.

Bone histological studies, now standard among paleontologists, have also cast light on other subjects dear to Nopcsa, including bird evolution. For example, in 2009 researchers from Germany, the U.S. and China reported in *PLOS ONE* that some early birds—the 140-million-year-old *Archaeopteryx* among them—have bone structures that show they grew up to a third as fast as living birds do, exhibiting a pattern more in keeping with "cold-blooded" reptiles than today's "warm-blooded" avians. Thus, some of the hallmark characteristics of living birds, such as their extremely fast growth rates, must have taken longer to evolve than scientists previously thought.

DINOSAURS ON THE MOVE

THE SIGNIFICANCE of Nopcsa's Transylvanian dinosaurs extends well beyond their implications for island-dwarfing theories, as the baron himself knew. Because most of Europe lay under the Tethys Sea during the Late Cretaceous, the Transylvanian specimens offer a rare glimpse of European dinosaurs from this period. Intriguingly, many of the forms found there—including the Hátszeg ornithopod *Telmatosaurus*—have counterparts only in

IN BRIEF

Franz Nopcsa (1877–1933) was a nobleman from Transylvania who loved and studied fossils.

Although best known for his personal and political exploits, he also pioneered techniques for fossil analysis and formulated theories about dinosaur evolution and dispersal around the globe.

Recent discoveries underscore that Nopcsa's scientific ideas were remarkably prescient.

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Asia or North America—not in the Southern Hemisphere. This distribution pattern suggests that Transylvania was an important bridge between Europe and the Late Cretaceous landmass comprising Asia and North America. Dinosaurs in Europe could cross the Tethys into Asiamerica, and vice versa, by hopping along Hátszeg and the other islands that formed an archipelago stretching from the European Alps to Southwest Asia.

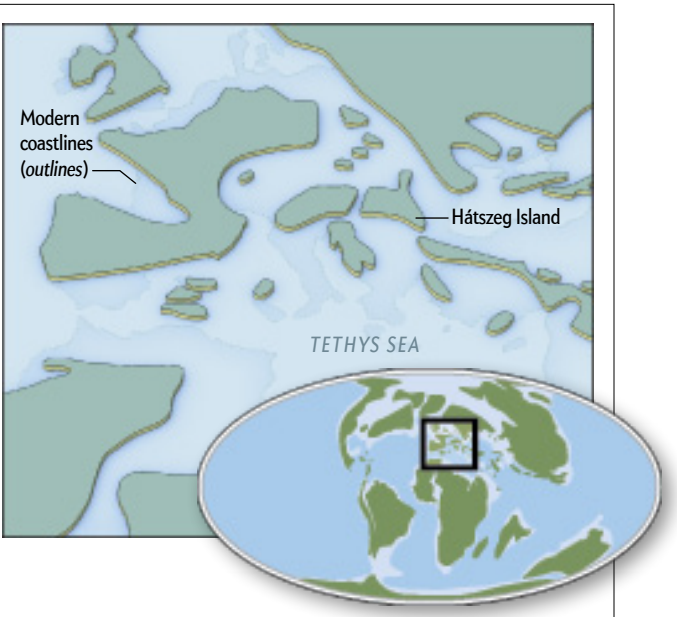
Geologic data published in 2010 in *Palaeogeography, Palaeoclimatology, Palaeoecology* have shown that because Hátszeg was close to both the European continental margin and to the open ocean, it probably provided a convenient stepping-stone for animals moving from east to west. Thus, the dinosaurs of Transylvania in general, and of Hátszeg in particular, will most likely prove critical to understanding the global distribution of dinosaurs just before the zenith of their diversity 66 million years ago—a heyday cut short by a cataclysmic asteroid impact that extinguished their kind.

Forged at a time when the sciences of paleontology and geology were still young and evolution was still hotly debated, Nopcsa's theories were astonishingly prescient. No doubt they benefited from his standing as a member of the aristocracy. Because of his wealth and influence at the court of the emperor of Austria-Hungary, Nopcsa had huge advantages over the average scholar of his day. He could travel freely throughout the empire on fossil-hunting expeditions and make regular pilgrimages to the great museums of Europe. He seemed to relish these escapes from court life, readily shedding his Viennese nobleman's finery for rough, native shepherd dress when he set out for the Balkans. Conversant in several Albanian dialects, Nopcsa would disappear into the hills of Albania, often for months or years at a time, with only his secretary and lover, Doda, for company. Although he produced an immense wealth of geologic, meteorological and ethnographic data over more than a decade of Albanian travel, much of it published in the leading scientific journals of the age, it is unlikely that Nopcsa took leave from the court purely for academic reasons: in 1923 he named a new 70-million-year-old fossil turtle he had collected in Transylvania *Kallokibotion bajazidi,* the genus name meaning "beautiful and round," in honor of Doda.

Unfortunately for Nopcsa, world events conspired to strip away his privilege. After the defeat in 1918 of Germany and its allies, including Austria-Hungary, Transylvania was ceded to Romania. He lost his estates and income as a result and began to worry about how he would continue to support his itinerant scientific lifestyle. To make ends meet, he accepted a position as head of the Hungarian Geological Institute and moved to Budapest. The constraints of institutional life did not suit the free-wheeling Nopcsa, however, and after just a few years he left his post to resume traveling with Doda by motorcycle in the Alps and in Italy, searching for fossils and mapping geologic features. To raise money to live on, he sold most of his fossil collection, including his treasured Transylvanian dinosaurs, to the British Museum of Natural History (now known as the Natural History Museum in London), a place he once had visited regularly as an honored scientific guest.

In the months before he died, Nopcsa received an invitation to address the Geological Society in Antwerp, Belgium. Although he was running a high fever, he made the trip. But he fell seriously ill the night before he was due to talk. Nevertheless, with no preparation, he delivered a lecture on the geology of Albania in French to a packed hall. "Whenever I talk," he later wrote to a friend back in Budapest, "the room is filled mostly with ladies who hope for fewer scientific explanations than adventure stories." Surely the swashbuckling dinosaur baron was happy to indulge them.

Alas, Nopcsa's life ended in tragedy. On April 25, 1933, the great fossil hunter, by now destitute and depressed, served Doda a drug-laced cup of tea and then fatally shot his sedated lover in the head before turning the gun on himself. The heartbreaking suicide note he left for police said, "The reason for my suicide is my nervous system, which is at its end. The fact that I killed my long-term friend and secretary, Mr. Bajazid Elmaz Doda, in his sleep, without him having an inkling as to what was going on, was because I did not want to leave him behind sick, in misery and in poverty because he could have suffered too much." The baron may be long gone, but his scientific legacy continues to grow. SA



ANCIENT ISLANDS such as Hátszeg, formed by a sea that covered much of Southern Europe during the Late Cretaceous, served as stepping-stones for dinosaurs on the move and allowed them to evolve to a small body size.

Gareth Dyke is a paleontologist at the University of Southampton in England, where he studies the evolutionary history of dinosaurs and birds. He is writing a novel inspired by Baron Franz Nopcsa's life.

MORE TO EXPLORE

Was Dinosaurian Physiology Inherited by Birds? Reconciling Slow Growth in *Archaeopteryx*. Gregory M. Erickson et al. in *PLOS ONE*, Vol. 4, No. 10; October 9, 2009.

Small Body Size and Extreme Cortical Bone Remodeling Indicate Phyletic Dwarfism in *Magyarosaurus dacus* (Sauropoda: Titanosauria). Koen Stein et al. in *Proceedings of the National Academy of Sciences USA*, Vol. 107, No. 20, pages 9258–9263; May 18, 2010.

European Island Faunas of the Late Cretaceous—The Haţeg Island. Special issues of *Palaeogeography, Palaeoclimatology, Palaeoecology,* Vol. 293, Nos. 3–4; July 15, 2010.

Early Cretaceous (Berriasian) Birds and Pterosaurs from the Cornet Bauxite Mine, Romania. Gareth J. Dyke et al. in *Palaeontology,* Vol. 54, No. 1, pages 79–95; January 2011.

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SOURCES: "AN UNUSUAL DINOSAUR FROM THE LATE CRETACEOUS OF ROMANIA AND THE ISLAND RULE," BY HANS-DIETER SUES, IN *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES USA*, VOL. 107, NO. 35; AUGUST 31, 2010 (*island*); *THE CHANGING FACE OF THE EARTH*, BY BRUNO VRIELYNCK AND PHILIPPE BOUYSSE; UNESCO PUBLISHING/COMMISSION OF THE GEOLOGICAL MAP OF THE WORLD, 2003 (*world*)

Map by Emily Cooper

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SANDSTONE ESCARPMENT in southern Mongolia made headlines in the early 1920s, when paleontologists found dinosaur eggs there. In the 21st century the Flaming Cliffs continue to yield a rich lode of well-preserved fossils.

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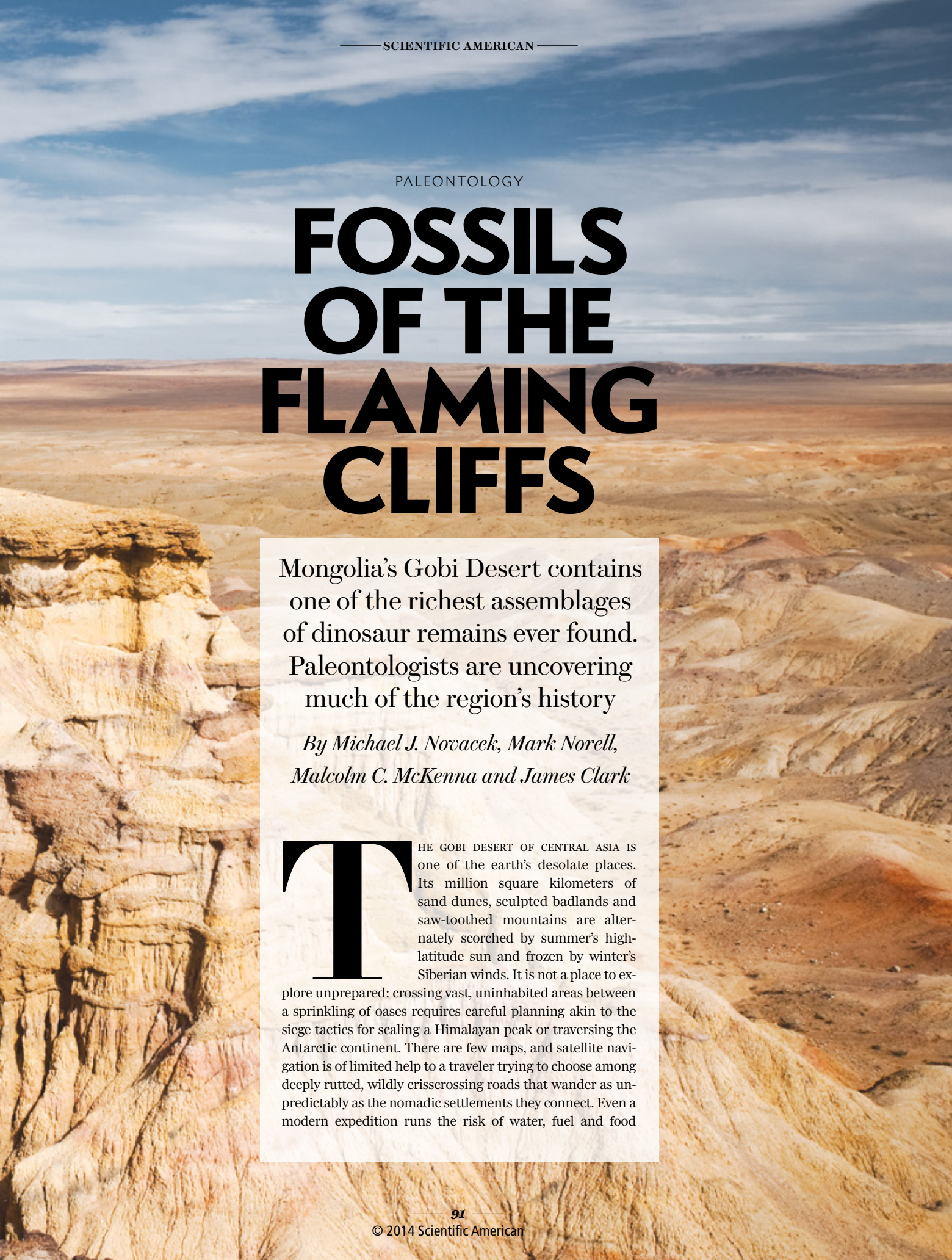

PALEONTOLOGY

FOSSILS OF THE FLAMING CLIFFS

Mongolia's Gobi Desert contains one of the richest assemblages of dinosaur remains ever found. Paleontologists are uncovering much of the region's history

By Michael J. Novacek, Mark Norell, Malcolm C. McKenna and James Clark

THE GOBI DESERT OF CENTRAL ASIA IS one of the earth's desolate places. Its million square kilometers of sand dunes, sculpted badlands and saw-toothed mountains are alternately scorched by summer's high-latitude sun and frozen by winter's Siberian winds. It is not a place to explore unprepared: crossing vast, uninhabited areas between a sprinkling of oases requires careful planning akin to the siege tactics for scaling a Himalayan peak or traversing the Antarctic continent. There are few maps, and satellite navigation is of limited help to a traveler trying to choose among deeply rutted, wildly crisscrossing roads that wander as unpredictably as the nomadic settlements they connect. Even a modern expedition runs the risk of water, fuel and food

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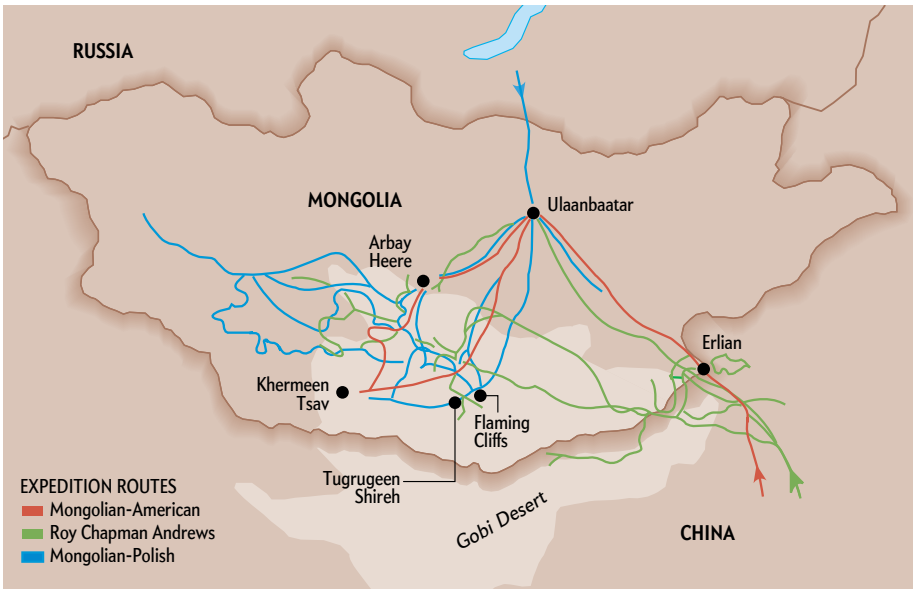
ROY CHAPMAN ANDREWS (*below, with dinosaur eggs*) led the first fossil-hunting expedition to the Gobi Desert in 1922. His group, which included camels and primitive cars, got lost several times; one such episode sparked the discovery of the Flaming Cliffs. Today expeditions rely on satellite navigation aids, but they face no less arduous conditions. Although paleontologists have mapped many fossil finds, much of the Gobi remains unexplored.



D I N O S A U R S !

shortages. Getting lost is not merely frustrating but a matter of serious danger.

Yet the Gobi is a paradise for paleontologists. Its eroding terrain exposes nearly complete skeletons of creatures hitherto known only through painstaking reconstructions from a few scattered bones. Our expeditions, jointly sponsored by the Mongolian Academy of Sciences and the American Museum of Natural History, have excavated dinosaurs, lizards and small mammals in an unprecedented state of preservation. Freshly exposed skeletons sometimes look more like the recent remains of a carcass than like an 80-million-year-old fossil. The skeletons and skulls we have found are often complete or nearly complete, in sharp contrast to the fragments typically recovered elsewhere.

No one knows why fossils in the Gobi are so well preserved. In other specimen-rich areas, such as the one that became the Rocky Mountains, streams or rivers carried animal remains to fossil sites, disarranging them along the way. The Late Cretaceous environment in the Gobi, however, may have been much as it is today: open valleys of sand dunes and cliffs, sparsely watered by small, seasonal lakes or streams. Indeed, indications of ancient sand dunes can be observed in rock sections there.

It is also apparent that the animals were buried very soon after their death, before scavengers or weather had much time to get at them. Poorly sorted layers of sandstone in the Cretaceous rock formations suggest deposits of the kind one would expect in violent sandstorms. In the early 1990s Tomasz Jerzykiewicz, then at the Geological Survey of Canada in Calgary, and his colleagues studied fossil beds in Chinese Inner Mongolia and found that vertebrate fossils are often embedded in these layers. Such storms might not have merely buried carcasses but killed animals as well. Entombed in a matter of minutes or hours, their remains emerge some 80 million years later, almost undisturbed.

STUMBLING ON *PROTOCERATOPS*

MONGOLIA WAS NOT ALWAYS recognized for its bounty of prehistoric material. During the late 19th and early 20th centuries, the Rocky Mountains region of western North America was the mecca for vertebrate paleontologists. Then, in 1922, Roy Chapman Andrews, a scientist from the American Museum of Natural History, led an expedition into the heart of the Gobi and changed the geography of the fossil world. Andrews chronicled his five expeditions in a remarkable narrative entitled *The New Conquest of Central Asia*. The romance and excitement of the enterprise foreshadowed the exploits of the movie character Indiana Jones. En route, the explorers were challenged by trackless dune fields, raging sandstorms and marauding bandits. Andrews's caravan of camels and spindly-wheeled Dodge motorcars was a logistic nightmare across the moonscape of the Gobi.

One of the most important discoveries in the history of scientific exploration came in the midst of such difficulties. Late in the

IN BRIEF

Beginning with a 1922 expedition that foreshadowed the adventures of "Indiana Jones," the Gobi Desert of Central Asia has been a paradise for paleontologists.
A site in southern Mongolia with red cliffs and spires, dubbed the Flaming Cliffs, has yielded a treasure trove of dinosaurs, including the first known cluster of dinosaur eggs.
Fossil hunters in the Gobi have also found rich assemblages of lizards, crocodilians, mammals and other vertebrates that are helping scientists understand the daily lives of these animals, reconstruct the past environment of the Gobi and trace lines of evolution.
Specimens found in the Gobi include skeletons of oviraptorid dinosaurs recovered sitting on their nests of eggs—the first nonavian dinosaurs to exhibit brooding behavior. Some dinosaur nests have been found in clusters, suggesting that these animals may have gathered in colonies like today's seabirds.

PRECEDING PAGES: THINKSTOCK; THIS PAGE: JOHNNY JOHNSON (*map*); BETTMANN/CORBIS (*Andrews*)

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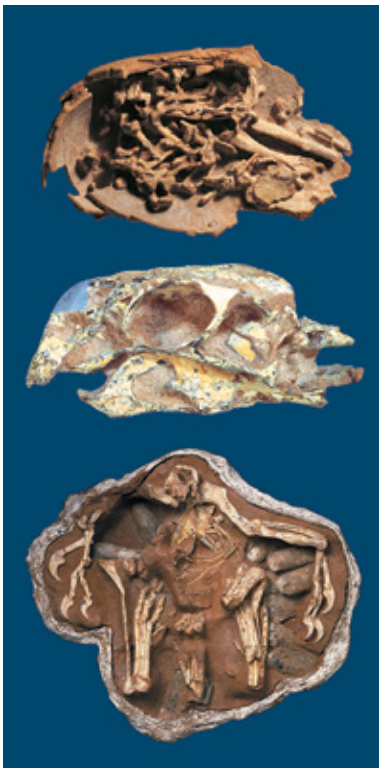
first field season of 1922, the expedition got off track. Team photographer J. B. Shackleford wandered toward an unassuming rock rim at the edge of a field. There he was startled to find a fantasy of red cliffs and spires—and fossils.

Within 10 minutes he had uncovered the first known skull of the *Protoceratops,* a parrot-beaked, shield-headed dinosaur that has since become a reference fossil of the Late Cretaceous of Central Asia. The crew recovered more bones and even a small egg, which they mistook for that of a bird. They returned the next summer to find an extravagance of dinosaurs, ancient mammals and other vertebrates, as well as the first known cluster of dinosaur eggs. Their findings, particularly the eggs, became front-page news. Andrews named the place the Flaming Cliffs, inspired by their magnificent red-orange glow in the late afternoon sun.

By the beginning of the 1930s Andrews, frustrated by a volatile political scene in Mongolia, gave up his exploration. The Gobi was inaccessible to Western interests for more than 60 years, leaving Soviet-bloc scientists to extend the work Andrews had begun. Between 1946 and 1949, joint Russian-Mongolian expeditions penetrated the Nemegt basin and uncovered rich badlands of Cretaceous and Cenozoic fossils there.

Zofia Kielan-Jaworowska, a world-renowned fossil-mammal specialist at the Institute of Paleontology in Warsaw, led a highly skilled and energetic Polish-Mongolian team to the Nemegt and other areas between 1963 and 1971. She and her colleagues produced a series of classic monographs and a magnificent display of dinosaurs and other fossil vertebrates at the Natural History Museum in the Mongolian capital of Ulaanbaatar. Since the 1960s Mongolian paleontologists have conducted extensive fieldwork both independently and in collaboration with Soviet (now Russian) scientists.

Westerners first returned after the development of Mongolian democracy in 1990. That summer our colleagues at the Mongolian Academy of Sciences invited us for a reconnaissance that paved the way for more ambitious expeditions during succeeding years.



OVIRAPTORID EGG (*top*) **contains an almost perfectly preserved embryo. The skull of a young troodontid (the family of predators that includes *Troodon*) was unearthed in the same nest; it is not clear how the interloper arrived. An adult oviraptorid skull (*middle*) was found at Ukhaa Tolgod in the western Gobi. This birdlike family of dinosaurs bore a resemblance to modern ostriches. Some oviraptorids (perhaps only one of the sexes) grew a large bony crest after they matured. A specimen (*bottom*) of the oviraptorid *Citipati* sits atop a nest of eggs.**

ROCKIES OF THE DESERT

IF ANYTHING, the contrast between the Gobi and other, more accessible fossil areas has increased since Andrews's time. A century ago, in the glory days of dinosaur hunting in the American West, prospectors encountered valleys and canyons where skeletons were exposed like corpses on a deserted battlefield, but today many prime dinosaur hunting grounds appear nearly exhausted.

The cumulative activities in Mongolia over the past 80 years, in comparison, do not approach those in the Americas. Erosion is still exposing a wealth of fossils even at sites well mined by Andrews and others. Moreover, the very difficulty and unexplored nature of the Gobi increases the chance that paleontologists may yet stumble onto wholly unexplored pockets of badlands.

Early in the 1993 season, with our Mongolian colleague, the now late Demberelyin Dashzeveg of the Mongolian Academy of Sciences, our field party struck out for an undistinguished set of red-brown sandstones on the north side of the Nemegt Valley, near the base of a jagged mountain range called Gilbent Uul. Previous expeditions, Dashzeveg said, had ignored this region in their rush to reach the more dramatic badlands of the western Nemegt Valley. We arrived at the area, struggled for a few kilometers along a wash, and established a bivouac where our heavy gasoline tanker and trailer buried itself in the sand.

The next morning we started prospecting the hills and gullies nearest camp. Within hours it was clear that we had come across one of the richest concentrations of fossils ever recovered from the age of the dinosaurs. In a basin less than two kilometers across, we found scores of dinosaur skeletons and egg nest sites weathering on gentle slopes. Intermixed with the dinosaur fossils were abundant smaller vertebrates—lizards and mammals—that were also key members of the ancient Cretaceous ecosystem.

The local name for the site of this bonanza is Ukhaa Tolgod ("Brown Hills"). Its natural amphitheater contained roughly 100 readily visible dinosaur skeletons, many of them in nearly pristine condition. During subsequent field seasons we selected the most desirable specimens. Among them are 25 skeletons of theropod dinosaurs. This group of agile carnivores runs the gamut from the enormous *Tyrannosaurus* and *Allosaurus* through fast-running dromaeosaurs such as *Velociraptor* (the villainous predator of *Jurassic Park,* a title some 60 million years out of date) to smaller birdlike creatures such as the oviraptorids. We also gathered an unprecedentedly rich collection of small vertebrates: more than 200 skulls of mammals—many with their associated skeletons—and an even greater number of lizard skulls and skeletons.

CRETACEOUS TREASURE TROVE

AS THE VARIETY OF OUR SPECIMENS makes clear, the flowering of terrestrial life during the Cretaceous of Central Asia was not limited to dinosaurs. The Gobi of 80 million years ago supported a wide variety of lizards, crocodilians and mammals. We have found specimens representing more than 30 species of lizard; some are extremely well

MARK NORELL (SPECIMENS PREPARED BY AMY DAVIDSON) (*top and bottom*); MARK NORELL (SPECIMEN PREPARED BY WILLIAM AMAREL) (*middle*)

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preserved and display anatomical features that offer clues to the relations among major lizard families.

Probably the most spectacular of these is *Estesia*. Early one morning during a reconnaissance, we came across an exquisite, 20-centimeter-long skull with knife-edged teeth half embedded, like a bas-relief, in a vertical slab of sandstone. At the time we thought it belonged to a small carnivorous dinosaur, but later examination determined that the skull was that of a wholly new kind of large predatory lizard, closely resembling the Komodo dragon of today. We named the species after Richard Estes of San Diego State University, the world's foremost authority on fossil lizards before his death in 1990.

Estesia is a very primitive animal and as such is significant for understanding the family tree of the varanoid lizards (the group that includes the Komodo). The skull has an unusual series of canals at the base of the teeth that suggests *Estesia* injected poison into its prey. This lethal weapon is not common to living varanoids but is found in the Gila monster of the southwestern U.S. and northern Mexico.

We have since uncovered fragments of *Estesia* in other sites where smaller lizards, tiny mammals and dinosaur eggshells are common. Modern varanoids are noted for their voracious and wide-ranging appetites. It is likely that *Estesia* ate smaller vertebrates, small dinosaurs and possibly dinosaur eggs.

Although much of the Cretaceous Gobi was dry, water must have been abundant in at least a few places and times. We found occasional fossils of turtles, usually associated with aquatic habitats.

Some of the greatest treasures of the Cretaceous Gobi are easy to miss when scanning the slopes and gullies: the tiny skulls and skeletons of mammals. These fossils represent important precursors of the great mammalian radiation that followed the extinction of the dinosaurs at the end of the Mesozoic.

The bulk of scientific information on these earlier mammals comes from North American fossils, which are mostly fragmentary jaws and teeth. In fact, there are virtually no complete skulls of these Cretaceous mammals from North America. As a result, the Gobi assemblage, including our finds and those of earlier expeditions, surely represents the world's reference collection for Late Cretaceous mammals.

A small block recovered from Ukhaa Tolgod revealed six shrewlike placental mammals, each only a few centimeters long. Amazingly, the fossils consist of complete skulls attached to skeletons; such tiny bones are usually found separated or broken. These small creatures were probably buried rapidly after they had died.

We have found two basic groups of mammals. The first is the multituberculates, or "multis," as paleontologists call them. They are a curious array of animals with long front incisors and molars with a complex of bumps (tubercles) on the tooth crowns. The Mongolian Cretaceous multis offer by far the best accumulation of skeletal material for examining the family trees of these creatures.

Multis can be thought of as the rodents of their time, even though they are in fact only distantly related to modern groups of mammals. Their rodentlike adaptations are a sign of convergent evolution with the rats, mice and squirrels familiar today. The multis thrived through the first several million years of the Paleogene period, after the dinosaurs had died out. They then dwindled in number and disappeared, replaced by more recent groups of similar habits.

The second group is the therians, ancestors of both marsupials and modern placental mammals (a category ranging from whales to bats, aardvarks and humans). These early therians consist of half a dozen shrewlike forms whose traits offer clues to the origins of later members of the group.

Mammals, lizards and other vertebrates are crucial to reconstructing the past environment of the Gobi and to tracing the main lines of evolution. But dinosaurs still occupy center stage in the public eye. The Cretaceous Gobi is unquestionably one of the world's great dinosaur hunting grounds. The fossils range from complete skeletons of *Tarbosaurus*—a fierce carnivore closely related to the North American *Tyrannosaurus*—to giant sauropods, duck-billed dinosaurs, armored ankylosaurs, frilled ceratopsian dinosaurs such as *Protoceratops* and a magnificent assemblage of smaller carnivores. Birdlike oviraptorids and dromaeosaurs such as *Velociraptor* are better represented in the stratified rocks of the Gobi than anywhere else in the world.

These remains have given rise to controversies but also to some definitive conclusions. Artists often depict *Velociraptor* hunting in packs like African wild dogs, for example, but there is no definitive proof that it was capable of such cooperative behavior. The predator's taste for *Protoceratops,* however, is more than a matter of speculation. In the late 1960s a group of Polish and Mongolian scientists at Tugrugeen Shireh, a white sandstone escarpment about

Illustration by Alfred T. Kamajian

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OVIRAPTORID, a large predatory dinosaur, stands near its nest by the bodies of two young troodontids (another fleet-footed predator). At the Gobi Desert's Ukhaa Tolgod site, the authors found an oviraptorid nest that contained two skulls of infant dinosaurs of the same family as ***Troodon;*** the interlopers might have been raiding the nest, they might have been brought by a parent oviraptorid to feed its young, or they might even have been laid in the nest surreptitiously (as the cuckoo does today) and incubated there.

80 kilometers west of the Flaming Cliffs, excavated one of the most remarkable pair of specimens in the history of paleontology. Two nearly intact skeletons—a *Protoceratops* and a *Velociraptor*—are preserved locked in mortal combat. *Velociraptor* clutches the lowered head of *Protoceratops* with its forelimbs and raises the killing hooks of its hind claws high against its prey's flanks. The "fighting dinosaurs," which may have met their end in one of the Gobi's sandstorms, are one of the great exhibits of the Natural History Museum in Ulaanbaatar.

Velociraptor skeletons are not only fascinating for the image they convey of intelligent, swift and lethal terrors. They offer clues to the evolutionary connection between birds and dinosaurs. *Velociraptor* and its relatives have many birdlike features, including the construction of the bony case of the brain and the design of the elongated limbs and digits. A nearly complete skeleton of *Velociraptor* unearthed at Tugrugeen in 1991 has a nearly complete braincase; in its details the architecture of the braincase is surprisingly similar to that of modern birds.

An unexpected discovery at Tugrugeen further amplified the proposed connection between dinosaurs and birds. We found a delicate skeleton that was identical, except for its smaller size, to one discovered by Mongolian scientists some years earlier. The animal, roughly the size of a turkey, has a remarkably gracile frame with long legs. In addition, the keel of the breastbone is extremely well developed. In modern birds, strong pectoral muscles that power the downstroke of the beating wing attach to this keel. Instead of long wing bones, however, this creature has stubby, massive forelimbs somewhat like those of a digging mole. The end of the arm and hand is appointed with a single, very large claw; hence, the scientific name bestowed on the animal is *Mononykus*—literally, "single claw."

Mononykus is a bizarre creature. Although it has no wings, it has features that suggest a closer relation to modern birds than the famous primitive bird *Archaeopteryx*. A detailed analysis of *Mononykus* favors the view that this creature was a flightless relative of modern birds.

That argument has drawn some criticism. Certain specialists claim *Mononykus* is simply a small dinosaur whose birdlike features are a product of convergent evolution. The weight of the evidence, however, does not favor convergence. The history of birds is marked by species (such as ostriches) that have lost their capacity for flight. Our *Mononykus* fossils do not show evidence of feathers, but it is only by some miracle of preservation that the fine Jurassic limestone entombing *Archaeopteryx* leaves impressions of tiny feathers. *Mononykus,* like most fossils, is not preserved in such unusual rock.

EGG HUNTER OR INCUBATOR?

EGGS OF BOTH DINOSAURS AND BIRDS, found in various parts of the Gobi, add another dimension to the fossil record. Some of the eggs contain small embryonic skeletons of the bird *Gobipteryx,* and others preserve the skeletal remains of a small embryonic dinosaur. In some places, several nests may be clustered on a hillside, and we infer that these nests mark a congregation of dinosaurs, much like a colony of seabirds today.

At Tugrugeen, we found 12 jumbled skeletons of *Protoceratops* on a flat not much larger than a putting green. A Sino-Canadian team also reported such accumulations of *Protoceratops* in Cretaceous rocks of northern China.

The *Protoceratops* sample includes several growth stages, providing a glimpse of this largely unknown aspect of dinosaur biology. Adults typically measure two meters long; in 1994 our team recovered some *Protoceratops* less than nine centimeters long. These skeletons are obviously those of very young individuals, possibly newborns.

As we make such discoveries, however, the picture of dinosaur life that emerges becomes more complex. Because *Protoceratops* is the most common dinosaur fossil in the region, paleontologists have long assumed that the many shells and egg aggregates found at the Flaming Cliffs and elsewhere belong to it. Yet evidence for this supposition has been unsatisfactory. None of the hundreds of dinosaur eggs collected have clearly identifiable *Protoceratops* embryos within them. Even the tiny skulls of *Protoceratops* we discovered cannot be positively linked with an egg of a particular type.

A find from Ukhaa Tolgod suggests that this assumption may have been wrong. The examination of a clutch of eggs containing dinosaur embryos found on our first day there revealed that an oblong, somewhat wrinkly egg usually attributed to *Protoceratops* held a nearly perfect oviraptorid skeleton. It appears likely that many of the eggs found at Ukhaa Tolgod (and possibly elsewhere) belong to these small carnivores rather than to the parrot-beaked, herbivorous Protos.

The Ukhaa Tolgod "nest" also contained two tiny skulls of a troodontid (possibly *Byronosaurus*) in the clump of eggs; bits of oviraptorid eggshell were associated with their bones. This curious coincidence of eggs, an oviraptorid embryo, and two very young or newborn troodontids has several plausible explanations.

Perhaps the young troodontids were honing their skills at an early age by raiding dinosaur nests. Alternatively, the parent oviraptorid may have been feeding the troodontids to her offspring, or the

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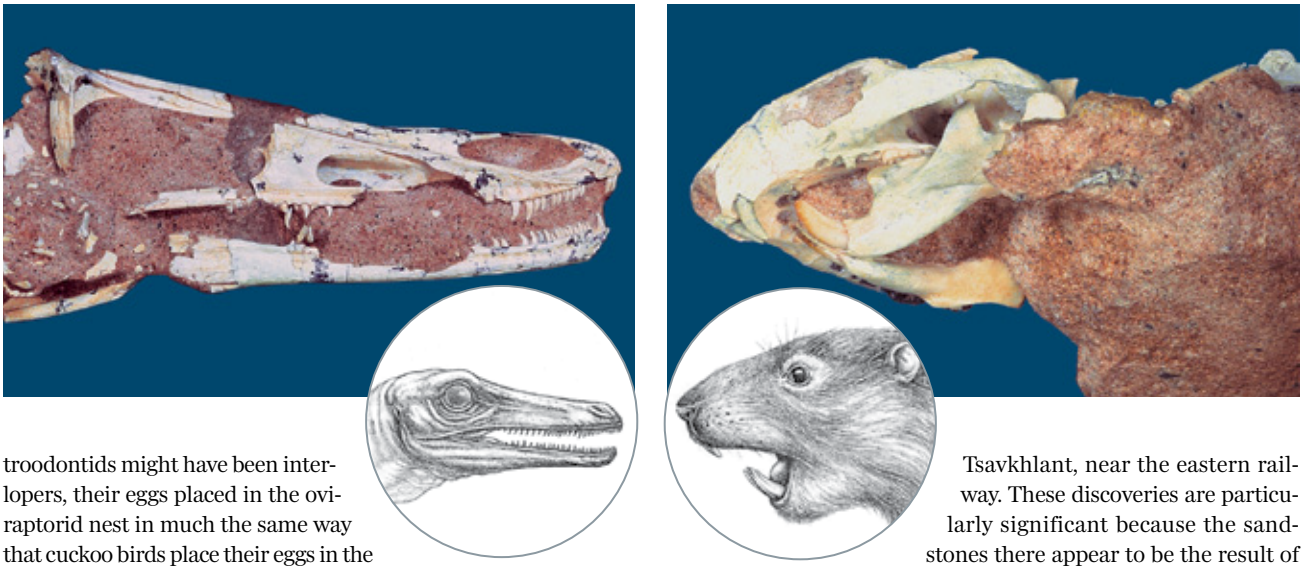

troodontids might have been interlopers, their eggs placed in the oviraptorid nest in much the same way that cuckoo birds place their eggs in the nests of other bird species.

This discovery puts an ironic twist on nomenclatural history. The Andrews expeditions applied the name *Oviraptor* to a skeleton at the Flaming Cliffs because it was found atop a clutch of eggs. They assumed that the eggs belonged to the common *Protoceratops* and that *Oviraptor* (literally, "egg hunter") was raiding a nest. Our find demonstrates that *Oviraptor* may not have been devouring eggs but rather incubating them.

DINOSAUR AND MAMMAL fossils from the Gobi are remarkably well preserved. The troodontid (*life-size photograph of skull and sketch, left*) was a small carnivore closely related to birds. The multituberculate skeleton (*right*) is almost completely intact even though some of its bones are barely half a millimeter thick; the skull is about 2.5 centimeters long. Multis, recognizable by the many bumps (tubercles) on the crowns of their teeth, were small mammals whose habits presaged those of rodents such as squirrels and mice.

TIME ELUDES

NESTING SITES and skeletons of birds, dinosaurs, mammals and other vertebrates all make up a fairly detailed picture of life in the Gobi during the Late Cretaceous. The evidence contributed by the Mongolian Academy–American Museum expeditions has been gathered by logging thousands of kilometers over a wide stretch of the Gobi rather than concentrating for a prolonged period on a single location or on a few sites. This method not only increases the chance of finding new fossil sites, it conveys a better sense of the rock sequence through comparison of fossil-bearing strata over a broad area. Thus, we can try to determine whether assemblages of animals and sediments representing a particular environment and time interval are widespread or confined to isolated outcrops.

For example, paleontologists have generally believed that the community of fossils in the Djadokhta Formation (a Central Gobi bed of brilliant red sandstones named for the Flaming Cliffs) is slightly older than that of the Barun Goyot Formation (which gets its name from an ancient settlement in the Nemegt Valley) in the western Nemegt. Both our findings at Ukhaa Tolgod and our broad survey, however, suggest that the two formations preserve contemporary, virtually identical fauna. We found an extension of this community in the magnificent red and vermilion beds of Khermeen Tsav, an isolated set of badlands in the arid desert west of the Nemegt region that strongly resembles the canyon lands of southern Utah.

We have also found fossils from the Djadokhta community, including the familiar *Protoceratops,* in an area called Khugene Tsavkhlant, near the eastern railway. These discoveries are particularly significant because the sandstones there appear to be the result of stream or river action, a situation more typical of North American sites than of the Gobi. It is slowly becoming clear that the animal community once thought to be localized at the Flaming Cliffs may have occupied a range of habitats.

The wide geographical separation of many sites, however, impedes comparisons. In addition, Gobi rock sequences are entirely sedimentary, without even traces of volcanic rocks. Thus, geologists cannot determine the age of these strata by analyzing their proportions of radioactive isotopes. Estimates of the age of various formations must rely on the similarity of the vertebrates to those of reference faunas on other continents and on correlations with invertebrate fossils from Cretaceous marine rocks in Central and East Asia.

In yet another twist, the rocks of the Gobi appear to be missing precisely those strata that currently hold the greatest public interest: no sections found thus far include the Cretaceous-Paleogene boundary, when the dinosaurs became extinct. Although the Gobi is richly endowed with early Paleogene mammal faunas, there seems to be a gap of at least several million years between these and the Late Cretaceous dinosaur faunas. Whatever cataclysm wiped out the dinosaurs, its mark on Central Asia has apparently been erased. If a continuous sequence could be located somewhere in the desert's vastness, it would make a formidable contribution to our knowledge concerning the dinosaur extinction and the subsequent rise of mammals.

The notion of finding the mass extinction in the Gobi is not just wishful thinking. Satellite navigation has already made a tremendous difference in the effectiveness of our work. We can plot the precise location of fossil sites and the routes that lead to them. We have also used satellite images as a prospecting tool. After we returned from Ukhaa Tolgod in 1993, Evan Smith, then at the Yale University Center for Earth Observation, enhanced red and brown spectral bands on computer-based satellite images by matching colors from photographs of the rocks there. The result is a map that shows with high precision the extent and contours of fossil-bearing strata.

MICHAEL J. NOVACEK (SPECIMENS PREPARED BY WILLIAM AMAREL) (*photographs*); MICK ELLISON *American Museum of Natural History (left inset)*; ED HECK *American Museum of Natural History (right inset)*

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During the 1994 season, we used these images as a field guide and simply drove to the latitude and longitude of a telltale cluster of red pixels, and some of these spots proved productive. We now have a useful paleontological atlas in a region where detailed topographic or geologic maps are virtually lacking. We also have something that Andrews lacked for his most important but serendipitous discoveries: a fairly decent road map of the Gobi.

Despite our new technology and the decades of insights into the evolution of vertebrates, exploration of the Gobi has much the same quality that Andrews experienced 92 years ago. The Flaming Cliffs we encountered on that first joyful day in 1990 were as Andrews described them—imposing, brilliant red in color and replete with fossils. Sandstorms that engulfed the 1920s expeditions returned to wreak havoc on our fragile campsites.

When the sandstorms clear, one can see from the top of the cliffs the mauve, furrowed mountains of the Gurvan Saichan. Beyond the mountains are hundreds of square kilometers of fossil-rich badlands whose existence Andrews could only have imagined.

EPILOGUE

By Mark Norell and Michael J. Novacek

MANY DISCOVERIES have been made since we wrote our 1994 article on the Gobi fossil hunt. Our summer 2013 expedition marked the 24th consecutive year of joint journeys by the Mongolian Academy of Sciences and the American Museum of Natural History. During the past two decades the important Ukhaa area has continued to yield many new and exciting fossils, including those in older rocks, in Lower Cretaceous beds in the north-central Gobi and, between 2002 and 2009, in Cretaceous sequences in the poorly explored reaches of the eastern Gobi near the Trans-Siberian Railway. This cumulative effort has revealed a broader and more graphic picture of life and death in Central Asia between 100 million and 75 million years ago.

Ukhaa Tolgod remains as perhaps the most significant discovery. It is a small, shallow drainage area of about four square kilometers, bordered by a serpentine line of low bluffs and adjacent flats where red rocks of the Djadokhta Formation are exposed. Geologic work has prompted reinterpretation of the accepted view that animals there were buried by gargantuan sandstorms. Based on detailed studies of sediments, our geologists David Loope and Lowell Dingus noted that the fossils at Ukhaa Tolgod are mostly restricted to beds that have no structure, suggesting that the dunes were stationary and possibly crowned with plants whose roots disrupted sand layers below the surface. This process of bioturbation was aided by the burrowing of small subterranean invertebrates, such as worms and insects, as well as larger burrowing mammals and lizards.

Loope and Dingus also observed that Ukhaa fossil beds contain streamers of pebbles too big to be windblown. Moreover, the sand has a high clay content, and the Mesozoic dunes are intercalated with water-resistant caliche layers. Hence, the dunes could not drain during heavy rainstorms; they instead acted as giant sandy sponges. At some point they became oversaturated and collapsed in large debris flows that covered sedentary animals, such as nesting dinosaurs, along with more active animals, making for phenomenal fossil preservation.

Many dinosaurs, lizards and mammals have been found at Ukhaa Tolgod. Most of them are fairly small, but there are hints (such as shed dinosaur teeth and footprints) that very large dinosaurs at least passed through. Some of the most common Ukhaa dinosaurs, such as ankylosaurs, were 4.5 meters long, and adult oviraptorids were a respectable three meters long. The remarkable dinosaurs also include groups of immature armored ankylosaurs, which may well have been gregarious because multiple skeletons are often found together.

Some of the most dramatic specimens are of the oviraptorid *Citipati,* which have been recovered sitting on their nests of eggs. Named after the Himalayan protector god of the funeral pyre, the creatures are the first nonavian dinosaurs known to exhibit avianlike brooding behavior. Additional specimens of the bizarre dinosaur *Shuvuuia* (previously called *Mononykus*) indicate that this animal is not a close relative of early birds but more primitive. Surprisingly, however, with one *Shuvuuia* specimen we found structural and biochemical evidence of feathers.

More than 600 mammal skulls, many with skeletons, have been recovered. This rich collection is critical to understanding the origins of modern mammal groups. Noteworthy is a form we named *Ukhaatherium,* which resembles the shrewlike species of the modern placental mammals but also retains primitive features such as the splintlike epipubic bones extending from the pelvis. The site has also yielded some of the best skeletons of *Deltatheridium,* an early relative of the marsupials, a group that includes opossums and kangaroos. Forms such as *Deltatheridium* and even more primitive species from the Early Cretaceous of northern China suggest that important branching events leading to the marsupial lineage occurred in the Mesozoic of Central Asia.

Between 2002 and 2009 we concentrated our efforts in the eastern Gobi, near our field operations of 1991. Additional study at Khugene Tsavkhlant, where we had earlier reported the ubiquitous *Protoceratops,* has indicated that this form is a much more primitive relative. We have also found interesting remains of mammals with low-crowned teeth. Right now we think this group is a distinct lineage that branched off just before the radiation of the modern placental mammals. In more recent years we have even ventured to the far western areas of Mongolia near the Chinese border to explore much older Jurassic beds.

Research progress has been aided by the technological trappings of 21st-century field exploration. Global Positioning System units, satellite phones and satellite imaging, portable computers, and digital cameras are standard equipment. We even have a solar-powered refrigerator to make camp life a little easier. The Gobi will doubtless continue to yield spectacular finds. SA

Michael J. Novacek, Mark Norell, Malcolm C. McKenna and **James Clark** have together explored fossil sites in the Gobi Desert under the auspices of the American Museum of Natural History and the Mongolian Academy of Sciences. Novacek is the museum's senior vice president for science, Norell is chair of the paleontology division, and McKenna, who was curator emeritus of vertebrate paleontology there and adjunct curator at the University of Colorado Museum, died in 2008. Clark, who worked at the American Museum of Natural History for three years, is now Ronald Weintraub Professor of Biology at George Washington University.

MORE TO EXPLORE

The New Conquest of Central Asia. Roy Chapman Andrews. American Museum of Natural History, 1932.

New Limb on the Avian Family Tree. Mark Norell, Luis Chiappe and James Clark in *Natural History,* Vol. 102, No. 9, pages 38–43; September 1993.

A Pocketful of Fossils. Michael J. Novacek in *Natural History,* Vol. 103, No. 4, pages 40–43; April 1994.

Dinosaurs of the Flaming Cliffs. Michael Novacek. Anchor Books, 1996.

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PALEONTOLOGY

DINOSAUR DEATH TRAP

On a trip to the Gobi Desert, a team of fossil hunters unearths a death scene that reveals new clues about how dinosaurs lived

By Paul C. Sereno

"ANOTHER SKELETON WITH A PERFECT SKULL!" I SHOUTED to the team, all of whom were face down on the quarry floor exposing other skeletons. In the years I had spent as a paleontologist, never had I seen anything like this. Our team of fossil hunters had been prospecting for only 15 days in the Gobi Desert of Inner Mongolia, but already we had uncovered a veritable graveyard of intact fossils.

Over the next few weeks we would apply chisel, pickax and bulldozer to the site, digging up more than a dozen examples of an ostrichlike dinosaur that was to become one of the most well known in the dinosaur world. But the story would soon grow far richer than a simple body count of fossil bones, as intact and well preserved as they might be. This group of individuals would reveal how these dinosaurs interacted with one another, how their society was built, as well as the circumstances surrounding their gruesome and untimely deaths. We were just beginning to uncover the first clues of this 90-million-year-old murder mystery. Little did I know that what we were about to learn would end up making this the richest site for a single dinosaur species I had ever encountered.

THE LURE OF THE GOBI

AMERICANS INEVITABLY associate dinosaur discovery in the Gobi with Roy Chapman Andrews, the swashbuckling expedition lead-

Illustration by James Gurney

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DOOMED TO DIE: Juvenile *Sinornithomimus* dinosaurs mired in mud 90 million years ago.

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er from the American Museum of Natural History in New York City. In the 1920s Andrews ventured into the desert regions of Outer Mongolia and returned to great fanfare with the first known dinosaur eggs and the sickle-clawed wonder *Velociraptor*. Andrews was not the only explorer combing the desert, however. At around the same time, Swedish explorer Sven Hedin was recovering unprecedented fossils from the southern half of the Gobi in Inner Mongolia, a region that is now part of China.

In the intervening years, scientists searching near Hedin's sites have uncovered dinosaur egg nests with brooding parents and sickle-clawed raptors that rival the best discoveries in Outer Mongolia. Yet scholars and public attention have favored Outer Mongolia; as a result, scores of international fossil expeditions have crisscrossed the area since it opened to the West more than a decade ago. In contrast, Inner Mongolia has remained relatively untouched.

I was a 27-year-old graduate student in geology in the middle of an around-the-world tour when I first visited Inner Mongolia in 1984—the first year that China allowed foreign tourists to travel in the country without an escort. After I arrived in the capital city of Hohhot by coal-powered steam locomotive, I visited the museum in the center of what was then a one-story town. Outside, dinosaur-age rock stretched for hundreds of kilometers west, flanking the fabled Silk Road linking the Mongolian steppe with the heart of Central Asia. When I returned to Beijing, I met with the now late Zhao Xijin, a professor at the Institute of Vertebrate Paleontology and Paleoanthropology and one of China's most accomplished fossil hunters, who had at the time already been responsible for discovering more than a dozen new species. We discussed exploring the area together at some time in the future. Some 16 years later the timing and circumstances finally aligned.

In 2000 I returned to Hohhot with Zhao to arrange the logistics of a major dig in the area. We stepped from the train onto the platform in Hohhot and were greeted by Tan Lin, a geologist and director of the Long Hao Institute of Geology and Paleontology in Hohhot. Looking much younger than his then 63 years, Tan energetically laid out the details of vehicles and supplies needed for a Gobi expedition the following spring. Fortunately, we would have no problem finding suitable expedition vehicles in Hohhot. The one-story town I knew had been replaced by a bustling metropolis with wide boulevards lined with flashing neon signs.

Tan suggested we revisit sites made famous by the fossil discoveries of Hedin and later expeditions. Certainly more fossils were there to be discovered. But I had other ideas. "Anywhere no one has been" was my refrain. Eventually the pull of the unknown won the day, and we decided to set out on the Silk Road in the spring, heading to the remote western reaches of the Gobi.

THE FIRST CLUES

BY MID-APRIL 2001 our 16-person crew composed of American, French, Chinese and Mongolian fossil hunters had gathered in Hohhot. We divided ourselves among four field vehicles and a truck packed with tons of supplies for the 700-kilometer trip along the banks of the Huang He (Yellow River) and out into the desert.

SPEED THE PLOW: Without this bulldozer, on loan from a nearby Chinese army base, the excavation would have taken months, not weeks.

We set up our first base camp not far from the tiny outpost of Suhongtu. The Gobi wind battered our iron-framed Chinese army tents, spraying a coat of silt and dust on everything inside. Hair soon stood erect as if gelled. Showers were out of the question, given the shortage of water and profound chill.

Every day we set out to hunt for fossils. Team members would walk for kilometers over the uneven terrain, searching for interesting finds that might be peeking out of the rock. With fossil hunting, it's good to be lucky, but it's better to be blessed with the "nose"—a natural talent for sniffing out fossils.

Montana State University paleontologist Dave Varricchio spotted the first major find—a three-toed footprint on the underside of a low ledge of rock. That footprint, notable for its short side toes, was small for a dinosaur, though bigger than his hand. We deduced that it was likely made by a large ornithomimid, or "bird mimic." Soon we would have no doubt about what made the print.

The area surrounding the camp was Late Cretaceous in age—about 90 million years old—according to a Chinese geology map printed some 25 years earlier. Apart from the footprint, our finds were limited to bones of small dinosaurs previously uncovered in the Gobi, and so we moved into a broad valley nearby where fossils were more plentiful. Soon team members were poking at several finds, including what was likely a primitive duckbill skull poking out of the surface. Another fossil appeared to belong to a small sauropod, the four-legged plant eaters that often grow to enormous size.

The most interesting site was a vertical wall of layered red and blue rock that was peppered with the leg bones of several relatively small dinosaurs. This was not a natural wall. Hewn by chisel and pick, it was the back wall of a fossil quarry. Someone had been there before us.

Tan explained that this site was originally found in 1978 during

IN BRIEF

An expedition in the Gobi Desert of Inner Mongolia turns up evidence of a 90-million-year-old graveyard, including the remains of more than a dozen fossilized skeletons of ostrichlike dinosaurs. **Evidence at the site** points to a unique and rare conclusion: the dinosaur fossils were not deposited at the site over millennia. Instead the dinosaurs all met their fate at the same time. **By studying this mass grave,** researchers have learned about the structure of dinosaur society, the ways in which these creatures interacted, and the division of labor between the adults and the juveniles.

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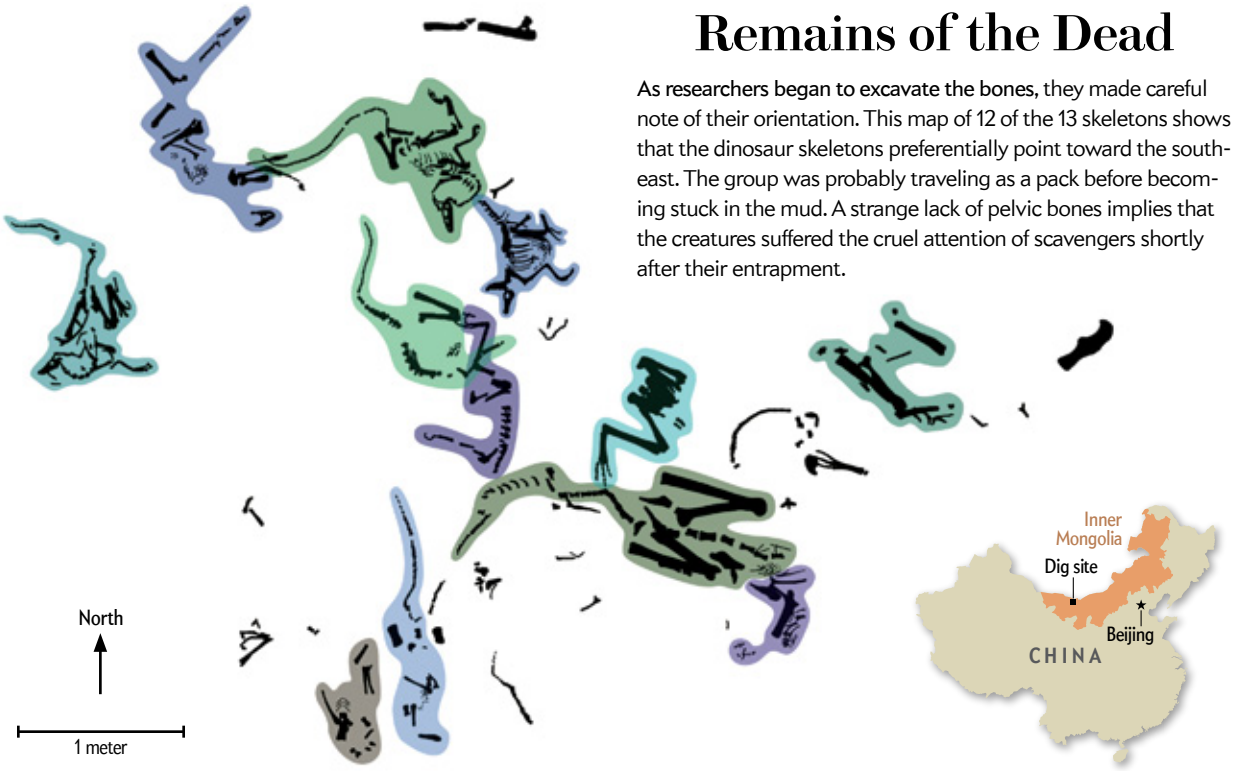
FOSSIL LAYOUT

Remains of the Dead

As researchers began to excavate the bones, they made careful note of their orientation. This map of 12 of the 13 skeletons shows that the dinosaur skeletons preferentially point toward the southeast. The group was probably traveling as a pack before becoming stuck in the mud. A strange lack of pelvic bones implies that the creatures suffered the cruel attention of scavengers shortly after their entrapment.



a mapping survey by a geologist and former classmate of his. "Look here," he said, pointing to a small bone symbol on the geology map. Using this map, Tan had guided a joint Chinese-Japanese-Mongolian expedition to this site four years earlier in 1997. Running short of time and materials, they had collected multiple skeletons but stopped before the excavation was complete.

In my backpack was a paper from 1999 on a new ornithomimid from the Gobi by a young Japanese paleontologist, Yoshitsugu Kobayashi, who at the time was a graduate student at Southern Methodist University. I now realized that the paper was based on finds from the quarry before me. Kobayashi and his colleagues had noted the presence of many fossils as well as their exquisite preservation; some fossils even included stomach stones—pebbles that ancient sauropods (and modern-day alligators, seals and birds) ingest to help grind food and aid digestion. In 2003 Kobayashi would name this dinosaur *Sinornithomimus dongi*. Yet mysteries remained: Why were so many fossils preserved in one small area? Did they all die at the same time or over millennia? And if they did all perish at once, how?

The quarry was located at the base of a small, rocky hill in a desolate windswept region of the Gobi. The horizon had turned gray brown—an early warning of an approaching dust storm. In the desert, these warnings are best measured in minutes, not hours. We raced for the field vehicles, hoping to dash back to camp while we could still navigate by the tracks we left on the way there. Within minutes the wind began to sling sheets of sand, dulling the paint on the lower reaches of our trucks.

The pore-filling dust and bone-chilling cold was offset at day's end by the camp cook, who regularly served seven-course meals for dinner—always a different seven from the night before. Fortunately, the camp was located not far from an army outpost, giving us access to fresh vegetables. Chinese cuisine, to my palate, is the best the world over. Equally renowned is Chinese beer, which we downed by the quart that season in celebration of our luck racking up noteworthy finds.

THE DEATH TRAP

WE RETURNED to that valley every day for the next few weeks, many of us devoted to unraveling the mystery of the ornithomimid quarry. One skeleton led to another, as our tools pushed the back wall of the quarry deeper into the hill. Others studied and sampled the cliff face, compiling a detailed log of the rocks entombing the graveyard.

When multiple individuals of a single species are preserved in one place, a paleontologist must ask whether that assemblage is natural—that is, was it a family group or herd congregating, as it might on a given day, only to be caught dead in its tracks? Most bone accumulations of a single species are not so interesting. Rather they are composed of unrelated individuals that, over some unknown length of time, died near a water hole or were washed in by a flood.

If we quickly bagged the remaining skeletons, the most interesting part of the story—how all these dinosaurs died—would be lost forever. Clues to the cause, circumstances and timing of death do not reside solely in the bones themselves but also in the position of skeletons, in the presence of tooth marks or splintered bone, and in the character of the sediment that is laid down before, during and after death. A crime scene, not a paleontologist's trophy trove, is how we must view such a quarry.

FROM "MUD-TRAPPED HERD CAPTURES EVIDENCE OF DISTINCTIVE DINOSAUR SOCIALITY," BY DAVID J. VARRICCHIO ET AL., IN *ACTA PALAEONTOLOGICA POLONICA*, VOL. 53, NO. 4, 2008 (*bone map*)

Map by XNR Productions (China)

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We soon came to believe that these animals all met their fate at the same time. The skeletons were not randomly distributed—all the bones seemed to point in the same direction. That could have been the result of a flood or a river carrying multiple sets of bones to the same place, but we could not find any evidence that the bones were moved in this way. All the skeletons were intact.

In addition, the thin-layered red and blue rock of the cliff face implied that the area used to consist of fine-grained mud and silt. We found spots in the infilled mud cracks, suggesting that the area went through wet and dry periods. Tiny, flat shells of freshwater creatures called conchostracans blanketed some of the skeletons, the flotsam from an expanding lake. Near the skeletons the mud was nearly pure, lacking the worm burrows and roots of a soil that supported plant life. All in all, the rock surrounding the skeletons suggested the ebb and flow of an ancient lake—an oasis in an otherwise dry area.

A collection of fossils such as this was unheard of—it was (and remains to this day) the only known Pompeii-like sampling of a dinosaur species. As the quarrying operation continued, we spent many hours musing on death scenarios. Perhaps these dinosaurs perished from a nearby volcano or succumbed to a flash flood? "Perhaps they just got stuck in the mud?" team member Gabrielle Lyon suggested, while outlining with a jeweler's needle the clenched digits of the foot of a fallen dinosaur. To me, the idea of a mud trap seemed a bit far-fetched. Though an experienced excavator, Lyon was an educator, not a paleontologist or geologist. Modern animals such as cows sometimes die near water holes—the large beasts get mired up to their kneecaps in mud and ultimately die of thirst, exposure and starvation. Yet it is extremely rare for entire herds to die this way (although sometimes it does happen to wild horses, noted Varricchio, the expedition's expert on taphonomy—the science of death and dying).

As we dug, more clues began to accumulate. Dave spotted V-shaped patterns on the cliff face near the horizon preserving the skeletons. The layers of mud were deformed downward, as if pulled by the passage of a thin object such as the claw on a dinosaur's toe. Was this evidence of a lethal dance in mud?

Unfortunately, we were not going to be able to dig for much longer. Our ornithomimid quarry was angling downward into the hill, getting more difficult to extract by the day. A complete excavation using the tools we had available would take months, if not years. Fortunately, we were soon to learn that in China, anything is possible.

On our day off we traveled out to the Chinese army outpost, where we were challenged to a game of basketball by the recruits. Professors Tan and Zhao watched from the sidelines, noticing the impressive heavy equipment parked nearby. Having befriended the soldiers during the basketball game, we took our case to officials at the base that evening, helped along with mind-numbing rounds of *baijiu,* a spirit that euphemistically translates to "white wine," even though it is served by the shot. A few days later a giant bulldozer arrived at the site.

As the blade trimmed off the top of the hill a few centimeters at a time, we followed in its wake, searching for fossils above the graveyard. "Stop!" shouted Jeff Wilson, who was hunched over a block tipped up by the monstrous blade. A paleontologist at the University of Michigan, Wilson had spotted some jaws and teeth. We picked through the tailings to each side of the last pass until we found all the missing pieces. Locked in that concretion just one human body length above the graveyard was a 45-centimeter skull of an unknown predator.

By the fourth day at the quarry, the bulldozer had removed the entire hill, its blade just above the graveyard. We resumed excavation until we unearthed the last of 13 individuals. Skeletons usually collapse on a flat surface to be buried in mere centimeters of sediment, but as we chipped the mudstone from the main horizon containing the skeletons, the hind legs of several dinosaurs plunged deep into the mud. Some of the otherwise perfectly preserved skeletons were missing hipbones. These individuals looked as if they were trapped in mud, only to suffer the attention of ancient scavengers.

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SCENES FROM A DIG (*from left*): Dave Varricchio searches for small bones; the author takes a pickax to the tough Gobi rock; a *Sinornithomimus* arm is found encased in rock; the team takes refuge from a sandstorm.

It was just what we would expect if a herd of dinosaurs on the move all became stuck on the same muddy shore. Lyon's hypothesis, drawn from the panic she must have sensed in the bones, was emerging as the most likely death scenario.

IN LIFE AND DEATH

BACK AT THE UNIVERSITY OF CHICAGO, members of my research team cleaned the skeletons one by one under the microscope, revealing a remarkable level of preservation. Not only were stomach stones preserved, but they seemed to retain the shape of the gizzard where they once pulverized plants. We also discovered a thin film of black carbon coating either side of the gizzard. The black material was the remains of the dinosaurs' last meal.

Additional evidence helped to confirm one of our hunches from the excavation. In the desert we had noticed that all the skeletons in the quarry were immature. At a field site the best way to measure a dinosaur's age is to examine the individual bones that constitute the backbone. Every vertebrae is made of a spool-shaped bone (the centrum) below and a curved structure (the neural arch) above. If these two parts are fully fused, the backbone is no longer growing, and the dinosaur is mature. All skeletons collected at Suhongtu had vertebrae preserved as two parts.

Yet this feature provided only a crude estimate of the dinosaurs' ages. Back at Chicago, we sliced bones into thin sections to count their annual growth rings as you would a tree. We learned that the skeletons ranged from one to seven years of age, with most ranging between one and two years old. This pattern told us two things. First, it meant that *Sinornithomimus* must have required about 10 years to reach maturity. And second, we realized that the herd at Suhongtu was a band of adolescents—dinosaur teenagers cruising in a pack.

With this realization we could put together the full history of the dinosaurs—not just the way they died, but the way they *lived* as well. Paleontologists have speculated about the social habits of half-grown dinosaurs, but the herd at Suhongtu provides the best evidence to date. Because maturation took about a decade in *Sinornithomimus,* juveniles had plenty of opportunities to congregate. Adults were busy with a range of activities during the breeding season—courtship, nest building, nest defense, brooding, and nurturing of hatchlings. Juveniles seem to have wandered about, fending for themselves as they went.

This particular group had met an untimely end. To a passing herd, the mud trap would have looked like many other areas along the lake's edge—mud that might record a footprint rather than swallow a foot. A central pair of skeletons most dramatically captures the 90-million-year-old tragedy. These two animals lay hopelessly trapped, their bodies collapsed sideways on the surface, one on top of the other, their feet deeply anchored in mud. Their skeletons were exceptionally complete except for their hipbones, which must have been pulled off by hungry scavengers. An isolated hipbone helped to confirm that scenario, the central portion of its blade crushed under the weight of an intruder's toe.

Then the water level rose, at least briefly, gently sealing in mud the graveyard and its tale of woe. SA

Paul C. Sereno is a paleontologist based at the University of Chicago. He has led expeditions to five continents and discovered more than two dozen new species of dinosaur. He is also co-founder of Project Exploration, a science outreach organization for urban youth.

MORE TO EXPLORE

Herbivorous Diet in an Ornithomimid Dinosaur. Y. Kobayashi, J. C. Lu, Z. M. Dong, R. Barsbold, Y. Azuma and Y. Tomida in *Nature,* Vol. 402, pages 480–481; December 2, 1999.

Mud-Trapped Herd Captures Evidence of Distinctive Dinosaur Sociality. D. J. Varricchio, P. C. Sereno, X. Zhao, L. Tan, J. A. Wilson and G. H. Lyon in *Acta Palaeontologica Polonica,* Vol. 53, No. 4, pages 567–578; 2008.

China 2001 (expedition led by Paul Sereno, Tan Lin and Zhao Xijin): http://paulsereno.uchicago.edu/expeditions/china_2001

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BIOLOGY

BLOOD FROM STONE

Mounting evidence from dinosaur bones shows that, contrary to common belief, organic materials can sometimes survive in fossils for millions of years

By Mary H. Schweitzer

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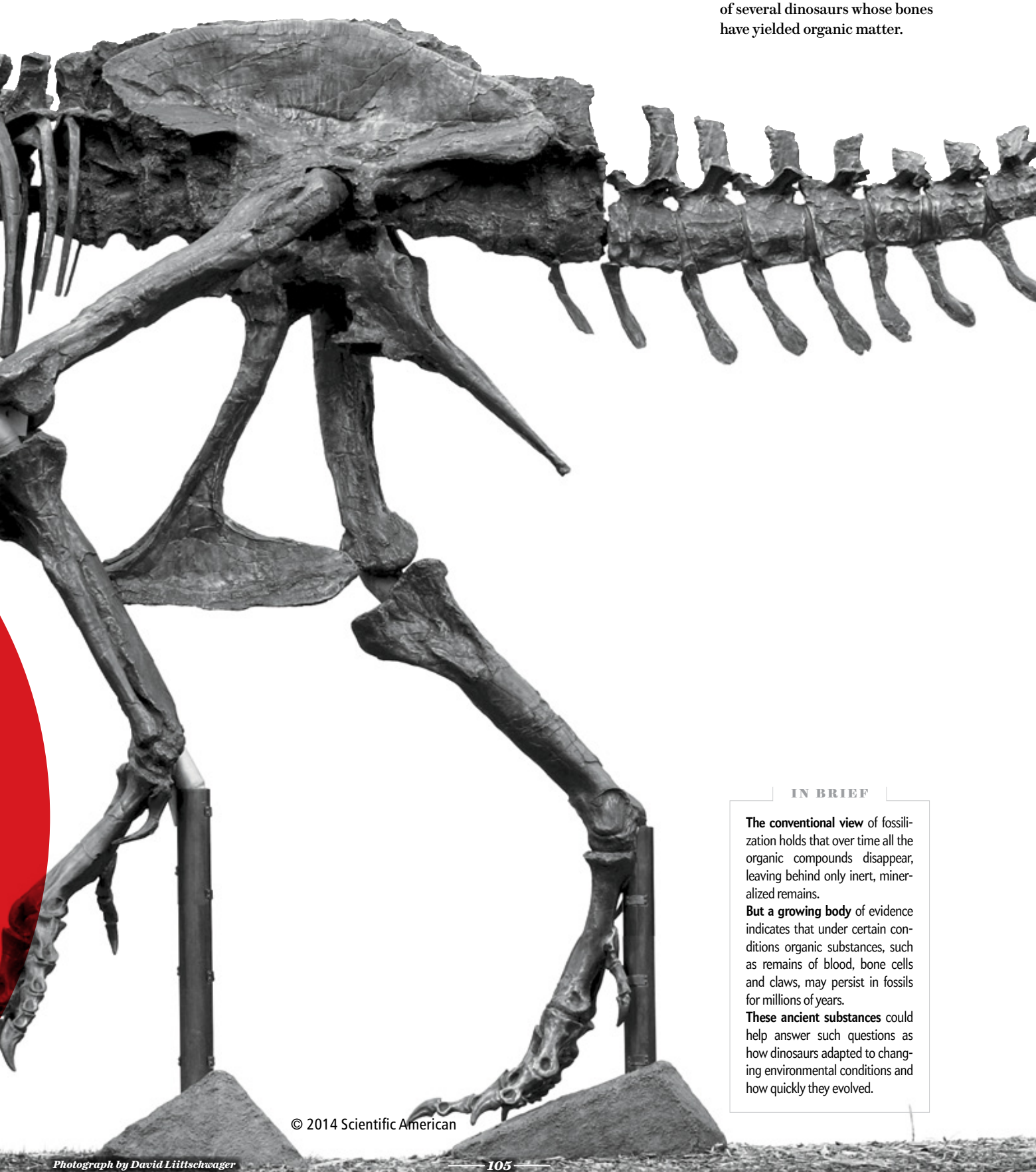

TYRANNOSAURUS REX known as MOR 555, a replica of which is shown here, is one of several dinosaurs whose bones have yielded organic matter.

IN BRIEF

The conventional view of fossilization holds that over time all the organic compounds disappear, leaving behind only inert, mineralized remains.

But a growing body of evidence indicates that under certain conditions organic substances, such as remains of blood, bone cells and claws, may persist in fossils for millions of years.

These ancient substances could help answer such questions as how dinosaurs adapted to changing environmental conditions and how quickly they evolved.

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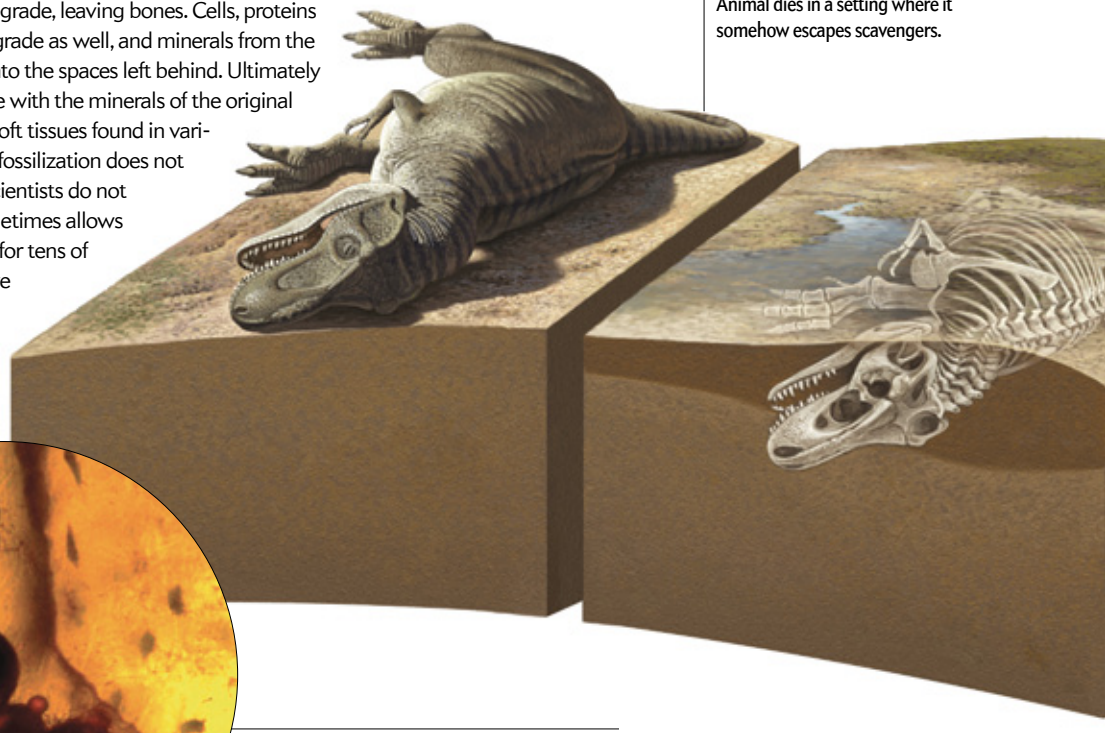
Photograph by David Liittschwager

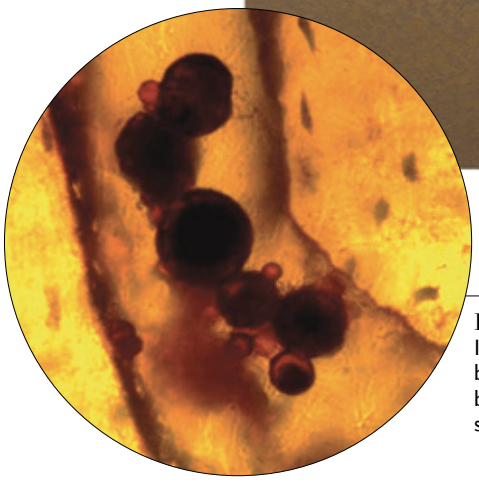
HOW FOSSILIZATION OCCURS

The Textbook Story, with a Twist

In the classic picture of how an animal becomes fossilized, the skin, muscles, guts and tendons degrade, leaving bones. Cells, proteins and blood vessels in bone degrade as well, and minerals from the surrounding sediment seep into the spaces left behind. Ultimately these create a solid composite with the minerals of the original bone. But cells, proteins and soft tissues found in various ancient bones show that fossilization does not *always* proceed in this way. Scientists do not understand exactly what sometimes allows organic substances to persist for tens of millions of years, but they have identified factors (*highlighted in red*) that may aid the preservation and recovery of these materials.



Death
Animal dies in a setting where it somehow escapes scavengers.



Early Discovery
In contrast to the typical look of fossilized bone under a microscope, a slice of a *T. rex* bone viewed by the author contained structures resembling blood cells.

FOR MORE THAN 300 YEARS PALEONTOLOGISTS HAVE OPERATED UNDER THE assumption that the information contained in fossilized bones lies only in the size and shape of the bones themselves. It was thought that when an animal dies under conditions suitable for fossilization, inert minerals from the surrounding environment eventually replace all the organic molecules—such as those that make up cells, tissues, pigments and proteins—leaving behind what is essentially a "cast" of the once living bones, now composed entirely of mineral.

My first indication that this fundamental tenet of paleontology might not always apply came when I was a relatively new graduate student at Montana State University, studying the microstructure of a *Tyrannosaurus rex* bone. As I peered through the microscope, what I saw—small, round, red and apparently nucleated structures, restricted to the blood vessel channels coursing through the bone—had not been previously noted, to my knowledge. They looked similar to the nucleated red blood cells of nonmammalian vertebrates. But seeing dinosaur blood cells was impossible, according to the conventional wisdom that shaped my discipline. After I sought opinions on the identity of the red spheres from faculty members and other graduate students, word of the puzzle reached Jack Horner, curator of paleontology at the museum and one of the world's foremost dinosaur authorities. He took a look for himself. Brows furrowed, he gazed

COURTESY OF MARY H. SCHWEITZER (*micrograph*)

Illustrations by Raúl Martin

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Burial
Carcass is covered with sediment before scavengers or weathering obliterates it, such as may happen when a river with a heavy sediment load washes over a floodplain.

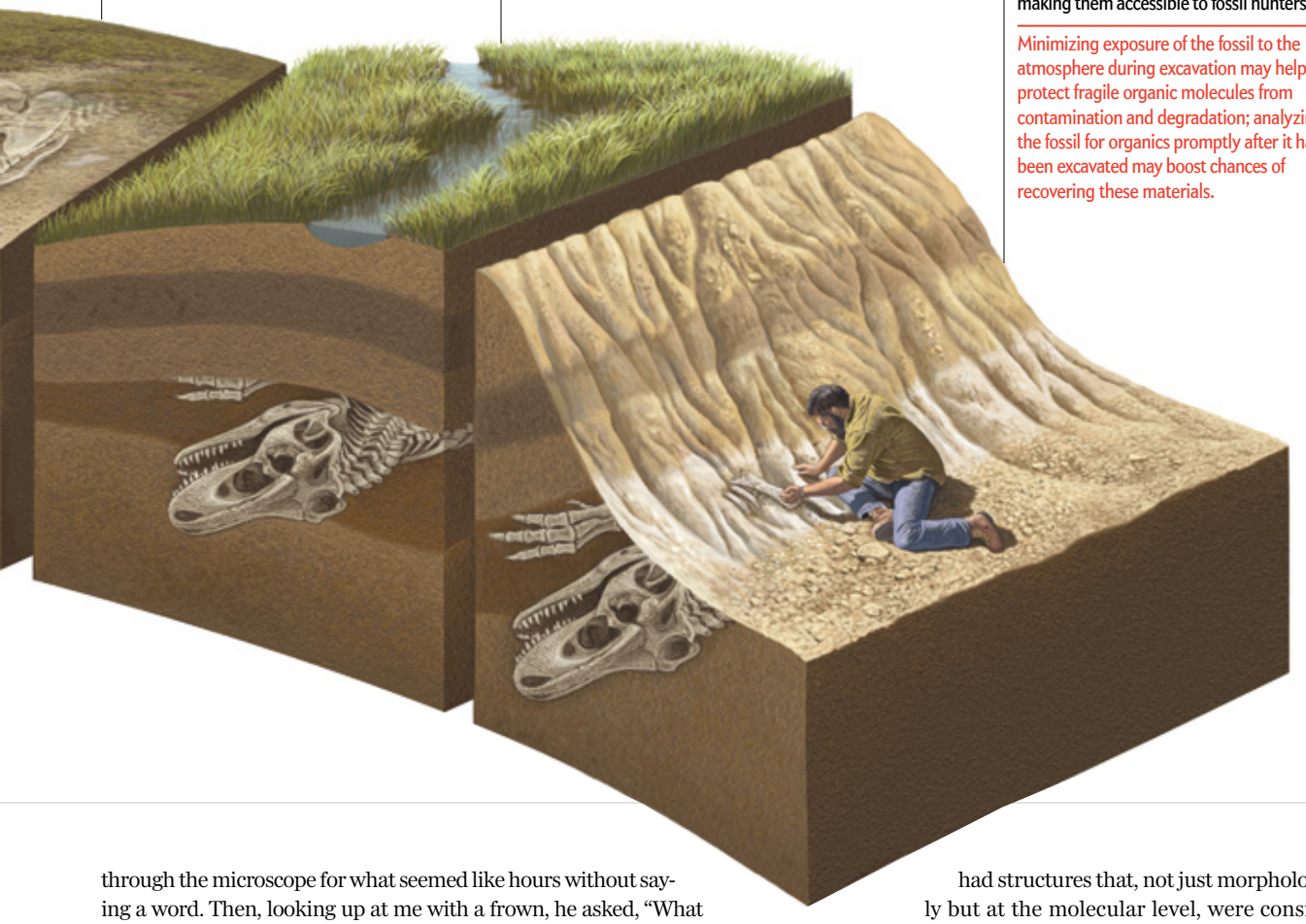
Sandstone sediments in particular seem to protect against complete loss of organic remains, possibly because the porous sands allow the corrosive fluids that form during decomposition to drain away.

Deeper Burial
Repeated deposition of sediments over millions of years buries the carcass far below the surface, where minerals from groundwater filter into the bones.

Deep burial (but not so deep that soft tissues are thermally altered) may promote preservation because it protects against oxidation, changes in pH and temperature, and exposure to ultraviolet radiation. Eventually the animal comes into chemical equilibrium with the underground environment, which may be key to preservation.

Exposure
Movements of the earth's crust uplift the sedimentary layers that contain the fossilized remains, and erosion exposes them, making them accessible to fossil hunters.

Minimizing exposure of the fossil to the atmosphere during excavation may help protect fragile organic molecules from contamination and degradation; analyzing the fossil for organics promptly after it has been excavated may boost chances of recovering these materials.



through the microscope for what seemed like hours without saying a word. Then, looking up at me with a frown, he asked, "What do *you* think they are?" When I replied that I did not know but that they were the right size, shape, location and color to be blood cells, he grunted. "So prove to me they aren't." It was an irresistible challenge, and one that continues to help frame my research.

Since that early discovery, my colleagues and I have recovered various types of organic remains—including blood vessels, bone cells and bits of the fingernail-like material that makes up claws—from multiple fossilized remains, indicating that although such preservation may not be common, neither is it a one-time occurrence. These findings not only diverge from textbook descriptions of the fossilization process, they are also yielding fresh insights into the biology of bygone creatures. For instance, bone from another *T. rex* specimen has revealed that the animal was a female that was "in lay" (preparing to lay eggs) when she died—information we could not have gleaned from the shape and size of the bones alone. And a protein detected in remnants of fibers near a small carnivorous dinosaur unearthed in Mongolia has helped establish that the dinosaur had structures that, not just morphologically but at the molecular level, were consistent with the feathers of modern birds.

FIRST SIGNS

EXTRAORDINARY CLAIMS, as the old adage goes, require extraordinary evidence. Careful scientists make every effort to *disprove* their own cherished hypotheses before they accept that their ideas are correct. Thus, for the past 20 years I have been trying every experiment I can think of to disprove the hypothesis that the materials my collaborators and I have discovered are components of tissues produced by once living animals.

In the case of the red microstructures I saw in the *T. rex* bone, I reasoned that if they were related to blood cells or their constituents (such as molecules of hemoglobin or heme that had clumped together after being released from dying blood cells), they would have persisted in some, albeit possibly very altered, form only if the bones themselves were exceptionally well preserved. At the macroscopic level, this dinosaur met that criterion. The skeleton, a nearly com-

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plete specimen from eastern Montana, known as MOR 555, includes many rarely preserved bones. Microscope examination of thin sections of the limb bones revealed similarly pristine preservation. Most of the blood vessel channels in the dense bone were empty, not filled with mineral deposits, as is usually the case with dinosaurs.

Next, I turned my attention to the chemical composition of the blood cell look-alikes. Analyses showed that they were rich in iron, as red blood cells are, and that the iron was specific to them. Not only did the elemental makeup of the mysterious red things (we nicknamed them LRRTs, "little round red things") differ from that of the bone immediately surrounding the vessel channels, it was also distinct from that of the sediments in which the dinosaur was buried. But to further test the connection between the red structures and blood cells, I wanted to examine my samples for heme, the small iron-containing molecule that gives vertebrate blood its scarlet hue and enables hemoglobin proteins to carry oxygen from the lungs to the rest of the body. Heme vibrates, or resonates, in telltale patterns when it is stimulated by tuned lasers, and because it contains a metal center, it absorbs light in a very distinct way. When we subjected extracts of whole bone samples to spectroscopy tests—which measure the light that a given material emits, absorbs or scatters—our results showed that somewhere in the dinosaur's bone were compounds that were consistent with heme.

One of the most compelling experiments we conducted took advantage of the immune response. When the body detects an invasion by foreign, potentially harmful substances, it produces defensive proteins called antibodies that can specifically recognize, and bind to, those substances. We injected extracts of the dinosaur bone into mice, causing the mice to make antibodies against the organic compounds in the extract. When we then exposed these dinosaur antibodies to hemoglobin from turkeys and rats, they bound to the hemoglobin—a sign that the dinosaur extracts that stimulated antibody production in the mice had included a molecule similar in some way to the hemoglobin in living animals.

None of the many chemical and immunological tests we performed rose to Jack's original challenge to "prove they aren't" blood cells from a *T. rex*. Yet we could not show that the hemoglobinlike substance was specific to the red structures—the available techniques were not sufficiently sensitive to permit such differentiation at the time I was conducting these studies. Thus, we could not claim definitively that these structures were derived from blood cells. When we published our findings in 1997, we drew our conclusions conservatively, stating that hemoglobin proteins *might* be preserved and that the most likely source of the protein was the cells of the dinosaur.

THE EVIDENCE BUILDS

THROUGH THIS INITIAL STUDY ON *T. REX,* I began to realize just how much fossil molecules could reveal about extinct animals. If we could obtain proteins, we could conceivably decipher the sequence of their constituent amino acids, much as geneticists sequence the "letters" that make up DNA. And like DNA sequences, protein sequences contain information about evolutionary relationships between animals, how species change over time and how the acquisition of new genetic traits might have conferred advantages to the animals possessing them. But first I had to show that ancient proteins were present in fossils other than the wonderful *T. rex* we had been studying. Working with Mark Marshall, then at Indiana University, and with Seth Pincus and John Watt, both at Montana State during this time, I turned my attention to two well-preserved fossils that looked promising for recovering other organic molecules.

The first was a beautiful primitive bird named *Rahonavis* that paleontologists from Stony Brook University and Macalester College had unearthed from deposits in Madagascar dating to the Late Cretaceous period, around 70 million to 66 million years ago. During excavation they had noticed a white, fibrous material on the skeleton's toe bones. No other bone in the quarry seemed to have the substance, nor was it present on any of the sediments there. They wondered whether the material might be akin to the strong sheath made of keratin protein that covers the toe bones of living birds, forming their claws.

Keratin proteins are good candidates for preservation because they are abundant in vertebrates, and the composition of this protein family makes them very resistant to degradation. They come in two main types: alpha and beta. All vertebrates have alpha-keratin, which in humans makes up hair and nails and helps the skin to resist abrasion and dehydration. Beta-keratin is absent from mammals and occurs only in birds and reptiles among living organisms.

To test for keratins in the white material on the *Rahonavis* toe bones, we employed many of the same techniques I had used to study *T. rex*. Notably, antibody tests indicated the presence of alpha- and beta-keratin, both of which are expressed in the claws of living birds and reptiles. We also applied additional diagnostic tools. One method detected amino acids that were localized to the toe-bone covering, which was supported by the identification of nitrogen (a component of amino acids). The results of all our tests supported the notion that the cryptic white material covering the ancient bird's toe bones was the remainder of its once lethal claws.

The second specimen we probed was a spectacular Late Cretaceous fossil that researchers from the American Museum of Natural History in New York City had discovered in Mongolia. Although the scientists dubbed the animal *Shuvuuia deserti,* or "desert bird," it was actually a small carnivorous dinosaur. While cleaning the fossil, Amy Davidson, a preparator at the museum, noticed small white fibers in the animal's neck region. She asked me if I could tell if they were remnants of feathers. Birds are descended from dinosaurs, and fossil hunters have discovered a number of dinosaur fossils that preserve impressions of feathers, so in theory the suggestion that *Shuvuuia* had a downy coat was plausible. I did not expect that a structure as delicate as a feather could have endured the ravages of time, however. I suspected the white fibers instead came from modern plants or from fungi. But I agreed to take a closer look.

To my surprise, initial tests ruled out plants or fungi as the source of the fibers. The fibers were hollow and contained tiny filaments consistent with the molecular structure of beta-keratin. Moreover, subsequent analyses of the composition of the strange white strands pointed to the presence of keratin. Mature feathers in living birds consist almost exclusively of beta-keratin. If the small fibers on *Shuvuuia* were related to feathers, then they should harbor beta-keratin alone, in contrast to the claw sheath of *Rahonavis,* which contained both alpha- and beta-keratin. That, in fact, is exactly what we found when we conducted our antibody tests—results we published in 1999.

EXTRAORDINARY FINDS

BY NOW I WAS CONVINCED that small remnants of original proteins could survive in extremely well preserved fossils and that we had the tools to identify them. But many in the scientific community remained unconvinced. Our findings challenged everything they thought they knew about the breakdown of cells and molecules. Test-tube studies of organic molecules indicated that proteins should not

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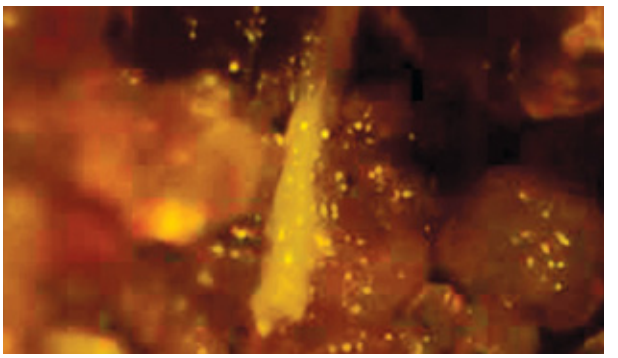
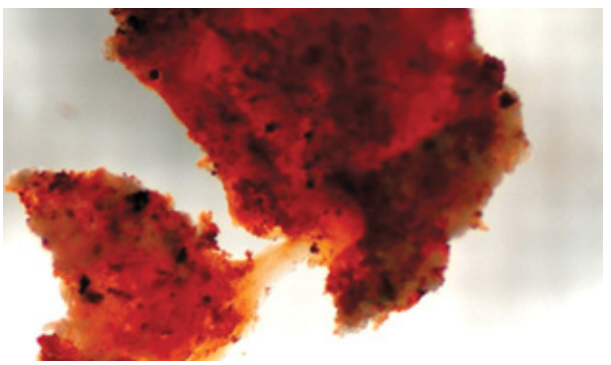
Ancient Organic Remains

Researchers have now recovered soft tissues from multiple fossils dating back tens of millions of years.

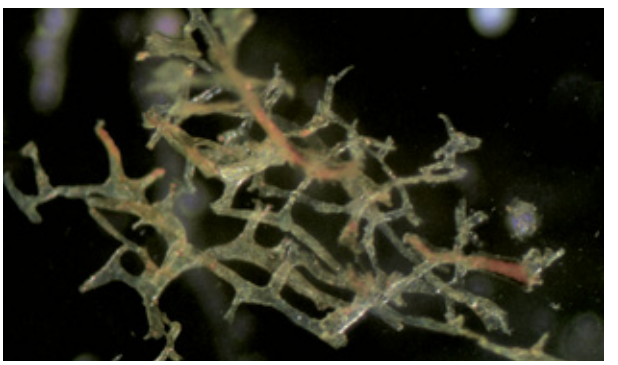
Toe bone of a bird called *Rahonavis ostromi,* which lived roughly 70 million to 66 million years ago in Madagascar, bears a white material that seems to be a remnant of the protein sheathing that covered the creature's claws.



Hollow filament (*center*) resembling a feather barb belonged to a small carnivorous dinosaur known as *Shuvuuia deserti* that inhabited Mongolia 83 million to 70 million years ago.



Medullary bone—a special tissue that appears for a limited time when a female's body readies eggs for laying—was found in a 68-million-year-old bone from a *T. rex* discovered in Montana.



Blood vessels—or their look-alikes—emerged when minerals were dissolved away from pieces of a common kind of bone, called cortical bone, in the Montana *T. rex.*

MARY LOU STEWART *Stony Brook University (toe bone);* MARY H. SCHWEITZER (*hollow filament and blood vessels*); FROM "SOFT-TISSUE VESSELS AND CELLULAR PRESERVATION IN *TYRANNOSAURUS REX*," BY MARY H. SCHWEITZER ET AL., IN *SCIENCE,* VOL. 307; MARCH 25, 2005 (*collagen from medullary bone*)

persist more than a million years or so; DNA had an even shorter predicted life span. Researchers had claimed previously that they had recovered DNA millions of years old, but subsequent work failed to validate the results, enhancing the controversy surrounding claims of recovery of very old molecules. The only widely accepted claims of ancient molecules were no more than tens of thousands of years old.

In response to this resistance, a colleague advised me to step back a bit and demonstrate the efficacy of our methods for identifying ancient proteins in bones that were old but not as old as dinosaur bone. Working with analytical chemist John Asara of Harvard University, we obtained proteins from mammoth fossils that were estimated to be 300,000 to 600,000 years old. Sequencing of the proteins using a technique called mass spectrometry identified them unambiguously as collagen, a key component of bone, tendons, skin and other tissues. The publication of our results in 2002 did not trigger much controversy. Indeed, the scientific community largely ignored it. But our proof of principle was about to come in very handy.

The next year a crew from the Museum of the Rockies finally finished excavating another *T. rex* skeleton, which at 68 million years old is the oldest one to date. Like the younger *T. rex* described above, this one—called MOR 1125 and nicknamed "Brex," after discoverer Bob Harmon—was recovered from the Hell Creek Formation in eastern Montana. The remote site has no vehicle access, so a helicopter ferried plaster jackets containing excavated bones from the site to the camp. The jacket containing the leg bones was too heavy for the helicopter to lift. To retrieve them, then, the team broke the jacket, separated the bones and rejacketed them. But these bones are very fragile, and when the original jacket was opened, many fragments of bone fell out and were collected and boxed up for me. Because my original *T. rex* studies were controversial, I was eager to repeat the work on a second *T. rex,* and this find presented the perfect opportunity.

As soon as I laid eyes on the first piece of bone I removed from that box, a fragment of thighbone, I knew the skeleton was special. Lining the internal surface of this fragment was a thin, distinct layer of a type of bone that had never been found in dinosaurs. This layer was very fibrous, filled with blood vessel channels, and completely different in color and texture from the cortical bone that constitutes most of the skeleton. "Oh, my gosh, it's a girl—and it's pregnant!" I exclaimed to my then assistant, Jennifer Wittmeyer. She looked at me like I had lost my mind. But having studied bird physiology, I was nearly certain that this distinctive feature was medullary bone, a special tissue that appears for only a limited time (often for just about

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two weeks), when birds are in lay. The special bone tissue exists to provide an easy source of calcium to fortify the eggshells, and when the last egg is laid, the medullary bone is quickly resorbed.

One of the characteristics that sets medullary bone apart from other bone types is the random orientation of its collagen fibers, a characteristic that indicates very rapid formation. (This same organization occurs in the first bone laid down when you have a fracture—that is why you feel a lump in healing bone.) The bones of any animal can be demineralized using mild acids to reveal the telltale arrangement of the collagen fibers. In living birds, removing the minerals from medullary bone should leave behind randomly oriented fibers. But this was dinosaur, not bird. I thought that almost all organics were gone from dinosaur bone, and if we let the reaction run too long, we would have nothing left, so Wittmeyer and I decided to lightly etch the surface. To our surprise, as the minerals dissolved they left a flexible and fibrous clump of tissue. I could not believe what we were seeing. I asked Wittmeyer to repeat the experiment multiple times. Each time we placed the distinctive layer of bone in the mild acid solution, fibrous stretchy material remained—just as it does when medullary bone in birds is treated in the same way.

Furthermore, when we then dissolved pieces of the denser, more common cortical bone, we obtained more soft tissue. Hollow, transparent, flexible, branching tubes emerged from the dissolving matrix—and they looked exactly like blood vessels. Suspended inside the vessels were either small, round red structures, very like those in the original *T. rex* that started me down this path, or amorphous accumulations of red material. Additional demineralization experiments revealed distinctive-looking bone cells called osteocytes that secrete the collagen and other components making up the organic part of living bone. The whole dinosaur seemed to preserve material never seen before in any dinosaur bone!

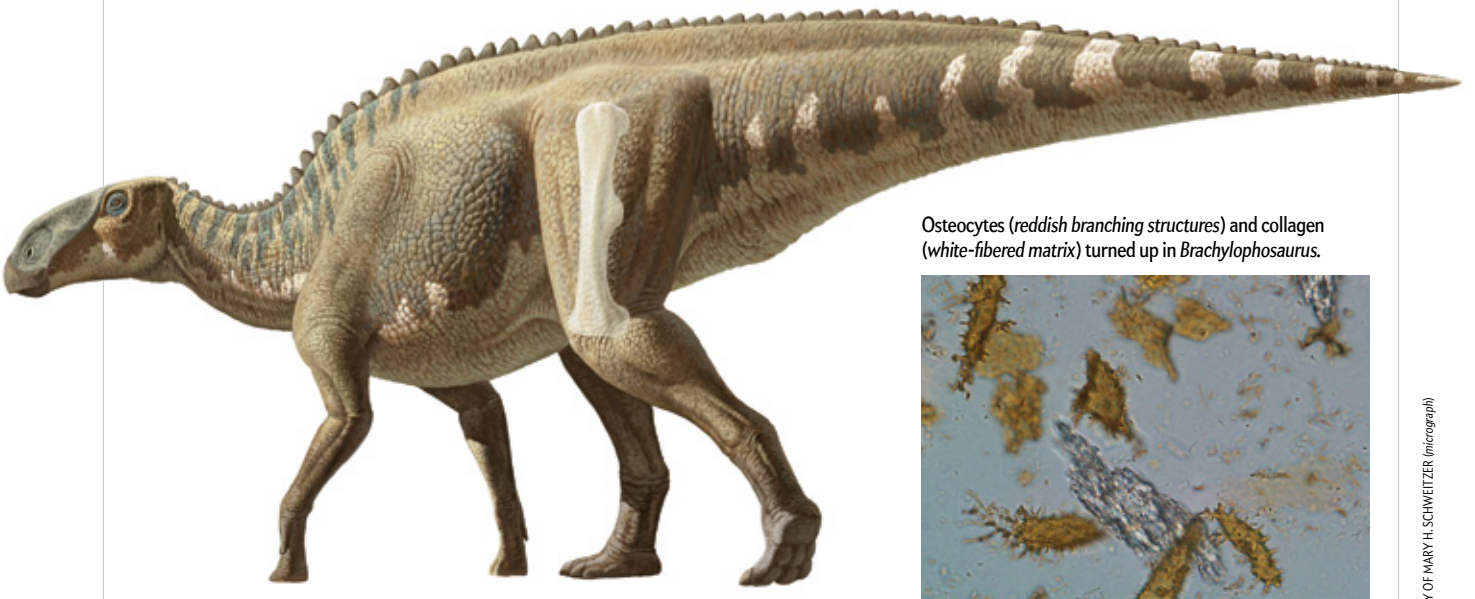
When we published our observations in *Science* in 2005, reporting the presence of what looked to be collagen, blood vessels and bone cells, the paper garnered a lot of attention, but the scientific community adopted a wait-and-see attitude. We claimed only that the material we found resembled these modern components—not that they were one and the same—because at that time we had no chemical data, only morphological data. And after millions of years, buried in sediments and exposed to geochemical conditions that varied over time, what was preserved in these bones might bear little chemical resemblance to what was there when the dinosaur was alive. The real value of these materials could be determined only if their composition could be discerned. Our work had just begun.

Using all the techniques honed while studying MOR 555, *Rahonavis, Shuvuuia* and the mammoth, I began an in-depth analysis of this *T. rex*'s bone in collaboration with Asara, who had refined the

CASE STUDY

Dissecting a Duckbill

Excavators working in eastern Montana recovered a well-preserved thighbone of the duck-billed dinosaur *Brachylophosaurus canadensis* in 2007. Microscopy revealed that the thighbone contained structures that resembled cells called osteocytes embedded in a matrix of white, fibrous material that looked like collagen protein (*micrograph*). Subsequent tests confirmed the presence of soft tissues and disproved the suggestion that the collagenlike and osteocytelike features might be derived from bacteria: extracts of the dinosaur's bone reacted with antibodies that target collagen and other proteins that bacteria do not make. And as would be expected if the bone harbored dinosaur protein, readouts from a technique called mass spectrometry, which identifies the amino acid sequences in proteins, looked much like those from modern birds, which are descendants of dinosaurs, and unlike those from bacteria.



Brachylophosaurus canadensis

Osteocytes (*reddish branching structures*) and collagen (*white-fibered matrix*) turned up in *Brachylophosaurus*.

COURTESY OF MARY H. SCHWEITZER (*micrograph*)

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methods we used in the mammoth study and was ready to try sequencing the dinosaur's far older proteins. This was a much harder exercise because the concentration of organics in the dinosaur was orders of magnitude less than in the much younger mammoth and because the proteins were very degraded. Nevertheless, we were eventually able to sequence protein fragments. And gratifyingly, when our colleague Chris Organ of Harvard compared the *T. rex* sequences with those of a multitude of other organisms, he found that they grouped most closely with birds, followed by crocodiles—the two groups that are the closest living relatives of dinosaurs.

CONTROVERSY AND ITS AFTERMATH

OUR PAPERS DETAILING the sequencing work, published in 2007 and 2008, generated a firestorm of controversy, most of which focused on our interpretations of the sequence data. Some dissenters charged that we had not produced enough sequences to make our case; others argued that the structures we interpreted as primeval soft tissues were actually biofilm—"slime" produced by microbes that had invaded the fossilized bone. I had mixed feelings about their feedback. On one hand, scientists are paid to be skeptical. On the other hand, science operates on the principle of parsimony—the simplest explanation for all the data is assumed to be the correct one. And we had supported our hypothesis with multiple lines of evidence.

Still, I knew that a single gee-whiz discovery does not have any long-term meaning in science. We had to sequence proteins from other dinosaur bones. When a volunteer accompanying us on a summer expedition found bones from an 80-million-year-old plant-eating duck-billed dinosaur called *Brachylophosaurus canadensis* ("Brachy" for short), we suspected the duckbill might be a good source of ancient proteins even before we got its bones out of the ground. Hoping that it might contain organics, we did everything we could to free it from the surrounding sandstone quickly while minimizing its exposure to chemicals, contaminants and the elements. Air pollutants, humidity fluctuations and the like would be very harmful to fragile molecules, and the longer the bone was exposed to any of these factors, the more likely contamination and degradation would occur.

Perhaps because of this extra care—and prompt analyses—both the chemistry and the morphology of this second dinosaur were less altered than Brex's. As we had hoped, we found cells embedded in a matrix of white collagen fibers in the animal's bone. The cells exhibited long, thin, branchlike extensions that are characteristic of osteocytes, which we could trace from the cell body to where they connected to other cells. A few of them even contained what appeared to be internal structures, including possible nuclei.

Furthermore, extracts of the duckbill's bone reacted with antibodies that target collagen and other proteins that bacteria do not manufacture, refuting the suggestion that our soft-tissue structures were merely biofilms. In addition, the protein sequences we obtained from the bone most closely resembled those of modern birds, just as Brex's did. We reported these findings in *Science* in 2009.

We have since demineralized bone from organisms ranging from modern chickens to Triassic material, collected in different environments and on different continents, to show that we can recover at least three of the four elements preserved in more than one dinosaur: blood vessels, vascular contents, osteocytes and collagen-based matrix. Also, we now have many independent lines of evidence indicating that those elongated, branching microstructures in the samples taken from Brex and Brachy are indeed the bone cells of once living dinosaurs. In one of the most convincing experiments, we exposed these microstructures to monoclonal antibodies that bind with a protein expressed in the osteocytes of living birds but not in the alligator osteocytes that we used as controls. We found that the antibodies did bind to the microstructures from both dinosaurs, in the same pattern that we saw in ostrich bone cells. Although we have data hinting at the presence of DNA inside these cells, our findings will not be conclusive unless we can obtain DNA sequences consistent with those predicted for dinosaurs—but the DNA may be too fragmented and altered to be sequenced.

One frequent criticism of our work is that it is inconsistent with models of cellular, tissue and molecular degradation—all of which predict life spans far shorter than 80 million years. So we conducted another set of experiments to address how, under naturally occurring conditions, these components might be preserved for such long time periods. We have noticed that in all cases where we are able to recover blood vessels and cells, we also see iron, embedded as tiny particles that are only visible under high-magnification transmission electron microscopy. We reason that this iron may have come from the breakdown of iron-rich hemoglobin, released by dying red blood cells. As the hemoglobin molecules break down, the unstable biological iron they release undergoes chemical reactions that unleash highly reactive free hydroxyl radicals. These hungry molecules attack tissues, stealing electrons to make themselves more stable and in the process causing cross-links to form between molecules of the tissue. This reaction, which is lethal in living organisms because the cross-linked molecules cannot function normally, acts much like placing tissues in formaldehyde—a preservative that also causes cross-links to form.

In experiments we have observed that blood vessels recovered from modern bone can remain stable in water at room temperature for more than two years if they are first briefly soaked in a lysate of red blood cells, whereas untreated blood vessels degrade in days to weeks. These results suggest that free radicals in the blood lysate may have stabilized the tissues against early degradation.

Our results have met with a lot of skepticism. They are, after all, extremely surprising, but they are also full of promise. The study of ancient organic molecules from dinosaurs could yield insights into how these great beasts evolved, how they responded to major environmental changes and ultimately what did them in. SA

Mary H. Schweitzer had already trained to become a high school science teacher when she took a class in paleontology for fun and reignited a childhood interest in dinosaurs. She then earned a Ph.D. in biology from Montana State University in 1995. Today she is a professor in the departments of marine, earth and atmospheric sciences and of biological sciences at North Carolina State University and curator of vertebrate paleontology at the North Carolina Museum of Natural Sciences.

MORE TO EXPLORE

Lita Preservation of Biomolecules in Cancellous Bone of *Tyrannosaurus rex*. Mary H. Schweitzer et al. in *Journal of Vertebrate Paleontology*, Vol. 17, No. 2, pages 349–359; June 1997.

Beta-Keratin Specific Immunological Reactivity in Feather-like Structures of the Cretaceous Alvarezsaurid, *Shuvuuia deserti*. Mary H. Schweitzer et al. in *Journal of Experimental Zoology*, Vol. 285, pages 146–157; August 1999.

Protein Sequences from Mastodon and *Tyrannosaurus rex* Revealed by Mass Spectrometry. John M. Asara et al. in *Science*, Vol. 316, pages 280–285; April 13, 2007.

Dinosaurian Soft Tissues Interpreted as Bacterial Biofilms. Thomas G. Kaye et al. in *PLOS ONE*, Vol. 3, No. 7, Article No. e2808; July 2008.

Biomolecular Characterization and Protein Sequences of the Campanian Hadrosaur *B. canadensis*. Mary H. Schweitzer et al. in *Science*, Vol. 324, pages 626–631; May 1, 2009.

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COMMENT

WHY DINOSAURS ARE IMPORTANT

Yesterday's big reptiles can help us figure out how the human era is shaping up **By Mary H. Schweitzer**

After more than 20 years as a professional paleontologist, I know how lucky I am to spend my days studying dinosaurs. In times when so many people can barely afford the basic necessities, how can I possibly justify using taxpayers' money to study animals that vanished millions of years ago? What can they teach us about today's world? Aren't they irrelevant to modern-day problems?

The truth is, paleontology is anything but irrelevant. The fossil record tells us that climate change is the planet's "normal" state. Does that mean the change we're seeing now is normal, or is the climate behaving in new ways because of human influence? How do we offset the damage we may have caused?

The best way to look ahead is to look behind, at those organisms, including dinosaurs, that survived extended climate change. The fossil record helps us compare today's climate changes and people's role in them with long-ago shifts before humans existed. And it has shown us five previous worldwide extinction events that occurred before the human era, enabling us to ask whether human activity is now causing a sixth global die-off. We could never consider such a question without knowledge of the distant past.

FEATHERED DINOSAUR from Liaoning Province, China

DINOSAURS, AMONG THE VERTEBRATES WITH THE MOST SPECIES, OFFER A RICH FIELD FOR STUDY.

More than 99 percent of the species that have ever lived are extinct. Each taxon we recover represents a different set of evolutionary experiments with different outcomes, and most can be studied only via the fossil record. Dinosaurs, among the vertebrates with the most species, offer a particularly rich field. A single dinosaurian lineage—the extant birds, with roughly 10,000 species—far outnumbers the 5,500 or so species of living mammals.

Occupying a temporal span of more than 200 million years and a geographical range that includes every continent and virtually every niche, dinosaurs have much to teach us. No other terrestrial vertebrates have ever remotely approached the great size of the sauropods, nor have they achieved the food-processing efficiency of the hadrosaurs, which had vertically stacked teeth that were replaced as they wore out. And we can only speculate on the diversity of flight ability among extinct avian dinosaurs such as the enantiornithines and the enigmatic, four-winged microraptors, with flight feathers not only on their forelimbs but also on their legs. The fossil record exhibits for us what is *possible* for vertebrate organisms, both in niche occupation and in biomechanical and morphological adaptations to these niches.

There is another, no less important reason to study dinosaurs: they fascinate even nonscientists. We can use this fascination to encourage young people to enter the sciences, at a time when that is more important than ever.

Engaging future researchers isn't the only way paleontology might energize other sciences. We are just beginning to decode the molecular information hidden in the fossil record. It's tricky: molecules recovered from fossils inevitably have been modified from their living state. But techniques for cracking the code might be useful in medicine, for example.

Even now we are losing irreplaceable data. When fossils aren't recovered properly, their scientific value is diminished. It's a dilemma: for farmers in rural China or nomads in Mongolia—even for ranchers in the dry, bleak High Plains of the U.S.—fossil finds can help pay for their children's education, put food on the table or warm their homes in winter. But the fossil finders seldom know or follow proper recovery methods.

It's not their fault. To be sure, greedy middlemen and wealthy buyers are part of the problem. But so is ignorance. Scientists need to take a more active role in educating the public—explaining why proper recovery of fossil material is so important. And we need tougher laws to deter illegal trafficking.

Scientists have a responsibility to raise awareness of the value of fossils—not just as collectibles but for the lessons we have yet to learn from the creatures that once walked this planet. Only by understanding the geologic record of diversity, adaptation and climate variability can we hope to face the challenges ahead. SA

Mary H. Schweitzer is a professor in the departments of marine, earth and atmospheric sciences and of biological sciences at North Carolina State University and curator of vertebrate paleontology at the North Carolina Museum of Natural Sciences.

MICK ELLISON *American Museum of Natural History*

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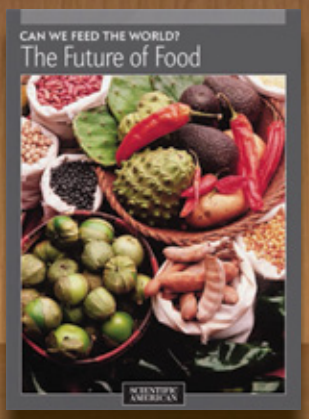

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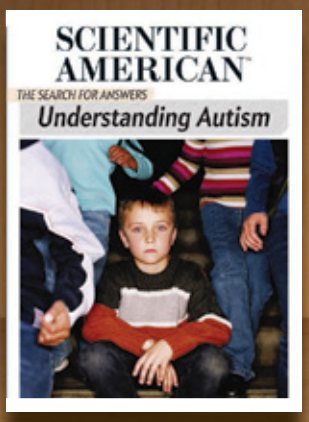

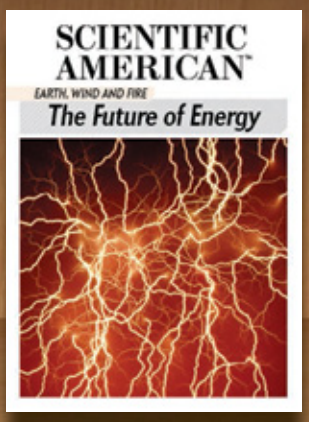

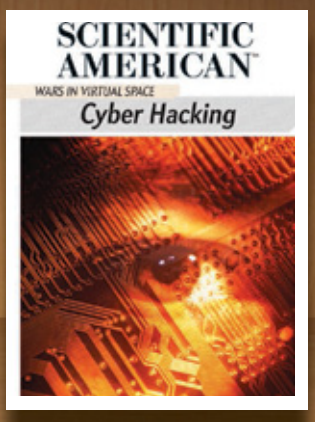

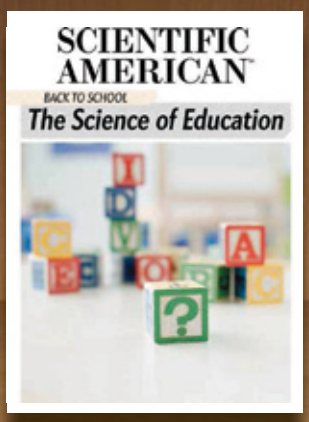

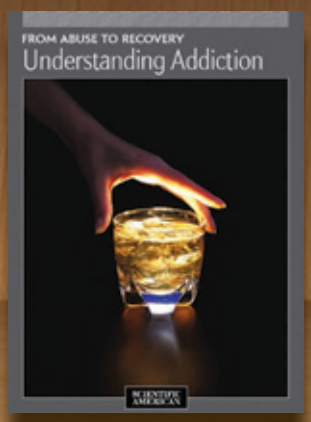

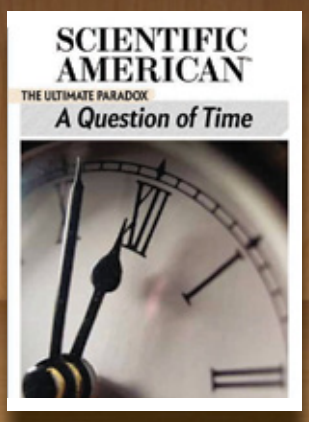

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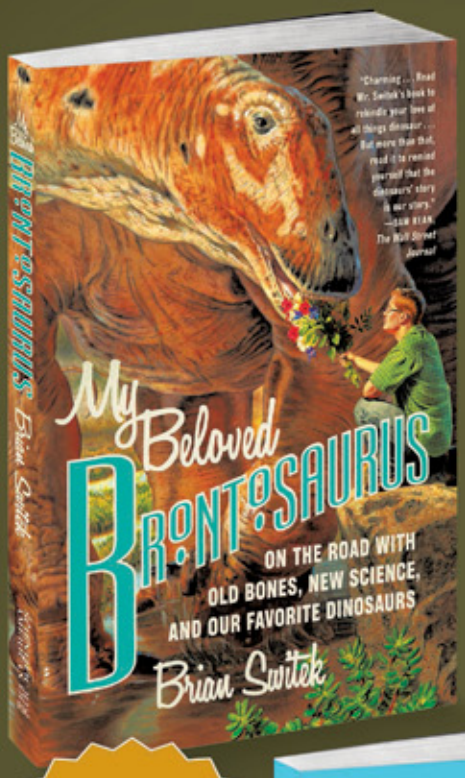

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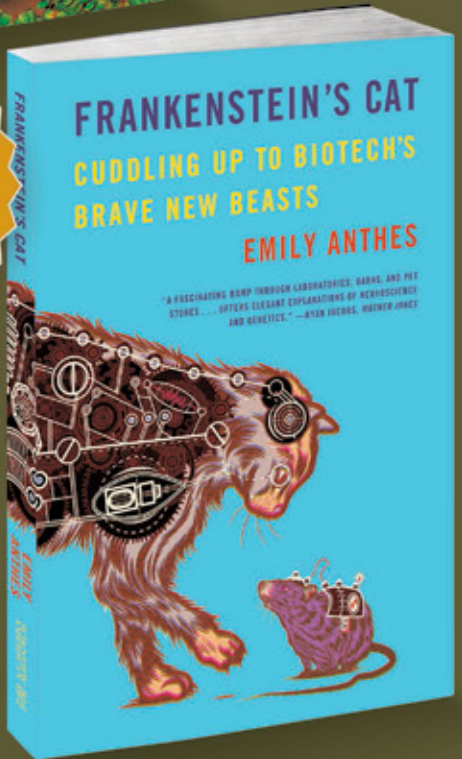

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